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MUSSELS (BIVALVIA: UNIONOIDEA) OF THE CUMBERLAND RIVER
Review of Life Histories and Ecological Relationships

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MUSSELS (BIVALVIA: UNIONOIDEA) OF THE CUMBERLAND RIVER

Review of Life Histories and Ecological Relationships

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PREFACE

The mussels of the Cumberland River Basin have been sporadically studied over the past 160 years. Despite this history of investigations, little is known regarding mussel habitat requirements and other aspects of their life history. Moreover, much of the existing information is in a diverse array of sometimes obscure documents with limited availability. The purpose of this report is to provide a synopsis of the information available on the life histories of the mussels of the Cumberland River Basin. This synopsis of the literature will be useful to biologists with a wide range of interests including taxonomists, ecologists and those involved in assessing mussel habitats and the impacts of water development projects and land-use practices on these habitats.

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ACKNOWLEDGMENTS

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INTRODUCTION

The Cumberland region long has been recognized as a center of molluscan endemism in North America (Binney 1885; Ortmann 1918, 1924a, 1925). Among the geographic faunal zones delimited for mussels by van der Schalie and van der Schalie (1950), the Cumberlandian fauna is the most speciose and possesses the greatest number of localized endemics. This area principally comprises the highland portions of the Cumberland and Tennessee river drainage basins. Although numerous studies have considered the aquatic Mollusca of the region, most have been faunal surveys or taxonomic reviews primarily concerned with the Tennessee River system (Appendix A). Two major studies extensively examined the mussel fauna of the Cumberland River (Wilson and Clark 1914; Neel and Allen 1964), while other investigations have surveyed more limited areas or tributaries (Appendix B). Recent statewide surveys of molluscs in Tennessee and Kentucky also have included records for the Cumberland River system (Bogan and Parmalee 1983; Starnes and Bogan 1988; Schuster 1988). Several species have been described from that river drainage (see Say 1829, 1831; Rafinesque 1831; Lea 1834-1874; Conrad 1836-1840) and specimens originating from the basin have been included in taxonomic and biogeographic reviews (e.g., Johnson 1978, 1980; Clarke 1981, 1985). Few, if any, studies have provided more than cursory considerations of ecology or reproductive biology for mussels indigenous to the Cumberland River system.

Most literature pertaining to the biology of freshwater mussels appeared during the first quarter of this century. At the time, mussels were harvested for pearls (Kunz 1898a,b) and mussel shells were the source of raw material for the pearl button industry (Coker 1919). The U.S. Bureau of Fisheries conducted extensive studies on mussels as a result of declining populations of commercially valuable species (Smith 1899, 1919; Coker 1914a,b, 1916, 1919; Coker, et al. 1921). Although much of the research included qualitative field surveys of existing populations (Appendix C), considerable effort was expended by the Bureau on the study of mussel production and propagation and on the identification of hosts (typically fish) for the parasitic mussel larvae (glochidia) (Appendix D). Ecological relationships were of concern (Simpson 1899; Lefevre and Curtis 1910b; Isely 1911, 1914b; Coker et al. 1921; Howard 1922; Ellis 1931a,b, 1936; also see Neves and Widlak 1987), but most of these data appear to have been collected ancillary to other field work and usually were not quantitative in nature (e.g., Wilson and Clark 1914). These early studies also tended to be limited to commercial species. Data were collected on other species, but most of this information was lost in a 1917 fire at the Bureau of Fisheries Laboratory, Fairport, Iowa (Fuller 1974). Recently, life history and ecological investigations have been conducted in response to further declines in populations, in attempts to preserve endangered and threatened species, and to integrate molluscs into conceptual models of aquatic ecosystems.

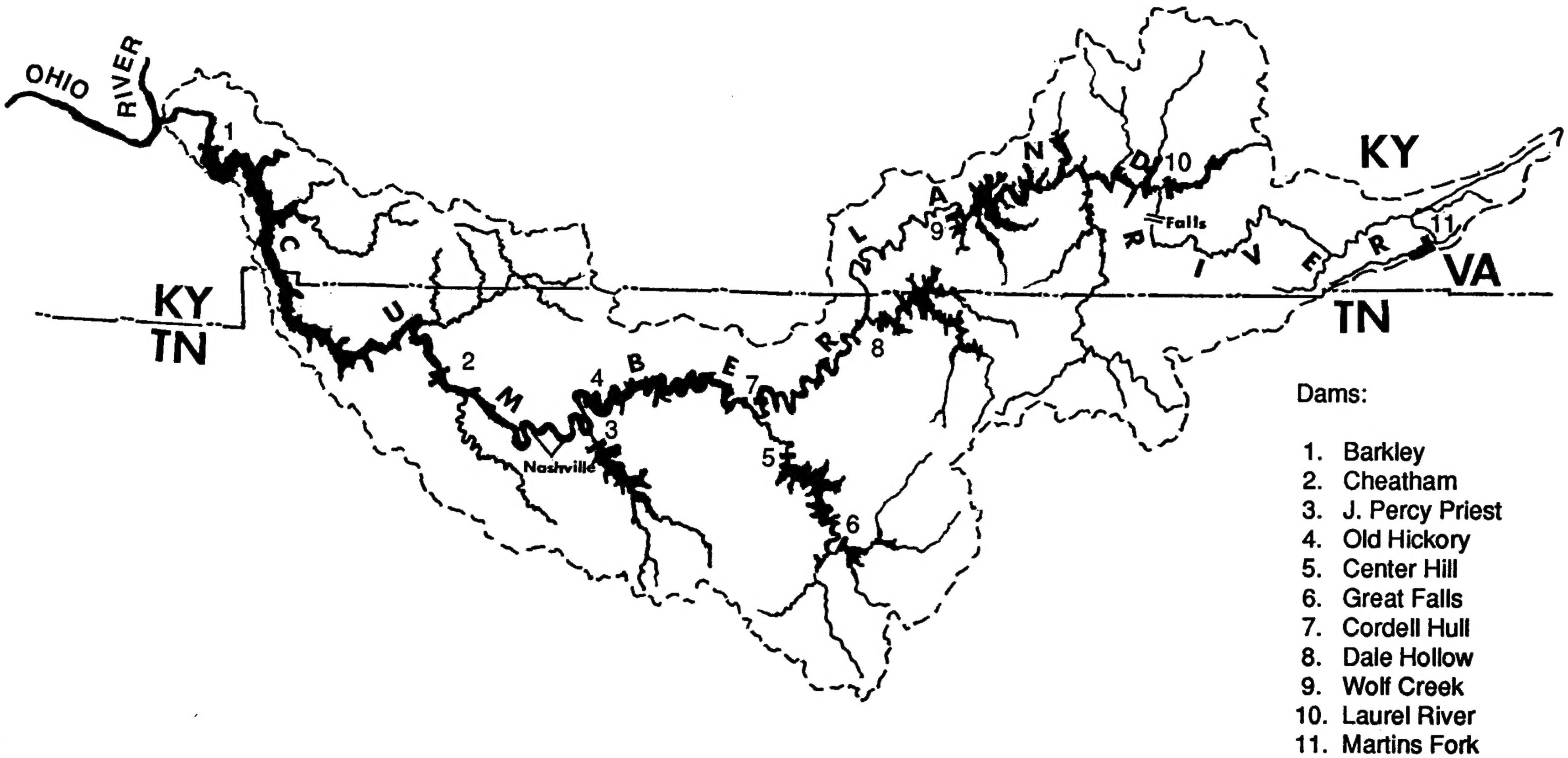

Figure 1. Cumberland River drainage basin and principal impoundments.

Species that occur within the Cumberland River basin have been subjects of both early and more recent studies. Most references on reproduction are from the older series of investigations. Although some quantitative assessments of population densities have been made (e.g., Tennessee Valley Authority 1976), no intensive, quantitative ecological studies on mussels have been conducted within the Cumberland River system. Incidental observations on habitat use, particularly in other regions, are available for some species (e.g., Wilson and Clark 1914; Baker 1928; Goodrich and van der Schalie 1944; Murray and Leonard 1962; Parmalee 1967; Buchanan 1980; Bogan and Parmalee 1983). As much of this information is dispersed through a rather diverse literature, this review is intended to compile data on reproduction/natural history and habitat use applicable to the mussel fauna of the Cumberland River basin.

FAUNAL ASSEMBLAGE

NOMENCLATURE

Taxonomy and, resultantly, nomenclature of the superfamily Unionoidea have been in a state of flux. Lack of reliable data has led to confusion and specific classifications. Subspecific designations often have reflected intra-population or ecophenotypic variation of shells, neither of which warrant subspecific status (see Mayr 1966). In-depth, systematic investigations (e.g., Davis and Fuller 1981; Davis et al. 1981; Kat 1983a,b, 1986; Smith and Wall 1984; W.R. Hoch, University of Michigan Museum of Zoology, pers. comm.) have been examining unionoid phylogenies and have contributed to better understanding of relationships. However, recent reintroduction of various early names (e.g., from Rafinesque 1820) have complicated nomenclatural problems. In several instances (e.g., Johnson 1980; Starnes and Bogan 1982; Gordon 1987a, 1989a,b), resurrected names have received published documentation and appear to be in accordance with the Principle of Priority [Article 24, International Code of Zoological Nomenclature (ICZN): Ride et al. 1985]. Other usages have not been justified properly and may not provide even synonymies of the subjugated names. On occasion, the validity of some names that have been used by investigators unfamiliar with taxonomy or nomenclature of freshwater mussels has been based solely on personal communications from an outside authority without prior published documentation.

Attempts are being made to resolve taxonomic and nomenclatural problems. In addition to systematic studies, applications have been submitted to the International Commission on Zoological Nomenclature concerning the usage of particular names (e.g., Bogan and Williams 1986; Gordon, in press). Recently, the American Fisheries Society published a checklist of common and scientific names for molluscs of the United States and Canada (Turgeon et al. 1988). However, this is a preliminary compilation and includes names of questionable validity, problems in gender agreement, and misspellings. As such, the nomenclature employed in the present manuscript differs somewhat from Turgeon et al. (1988) in an attempt to present an accurate accounting of species.

MUSSELS

Critical review of published records (see Appendix B; also Burch 1975; Johnson 1980), examination of museum specimens, and personal collecting indicate a historical fauna of 94 mussel species for the Cumberland River system (Table 1). Twenty-four species are Cumberlandian regional endemics, but only three of these--*Quadrula tuberosa*, *Pleurobema gibberum*, and *Alasmidonta atropurpurea* are restricted to the Cumberland River basin. The river can be divided into three faunal zones (see Wilson and Clark 1914; Ortmann 1924a). A lowland river morphology occurs downstream from Clarksville, Montgomery County, Tennessee. This area lacks Cumberlandian endemics but includes six species that are not distributed farther upstream (Table 2). The only record for the federally-endangered *Proptera capax* is from the confluence of the Cumberland and Ohio rivers (Sickle 1987). The majority of species occur in the middle section of the drainage basin, between Clarksville and Cumberland Falls, Whitley County, Kentucky. Eleven species have been reported from above the falls (Table 3); however, Wilson and Clark (1914) indicated that *Lampsilis ovata* had been introduced above the falls. There may have been some confusion among investigators in distinguishing *A. marginata* from *A. atropurpurea* and *Strophitus undulatus* from *Anodontoides ferussacianus*. *Alasmidonta atropurpurea* and *Anodontoides ferussacianus* recently have been collected from above the falls thus confirming their presence.

The faunal composition and distribution of mussels in the Cumberland River system has changed substantially over the last 60 years. While an undetermined number of species may have been extirpated due to activities such as reservoir construction, a few (e.g., *Obovaria retusa*, *Epioblasma obliquata* apparently persist as relict, non-reproducing populations (Tennessee Valley Authority 1976; Isom et al. 1979; Parmalee et al. 1980; Bogan and Parmalee 1983). At least nine species may be extinct and eight species are federally-listed as endangered (Table 1). Other species have been able to successfully cope with inundation in certain instances, e.g., sublotic zones--reservoir headwaters which are the tailwaters for upstream reservoirs and retain flowing-water conditions). In such areas, species composition may switch from dominance by strictly lotic-adapted species (e.g., *Quadrula fragosa*, *E. haysiana)* to species tolerant of lacustrine habitats (e.g., *Q. quadrula*, *Anodonta suborbiculata*).

FISH

Fish are integral in the reproductive cycle of unionoid mussels. The glochidial larvae of most North American mussels apparently are obligate parasites of fish during metamorphosis to the juvenile stage. With some unionoids, host specificity may be quite narrow (Howard 1914a). Compilation of available records (e.g., Lee et al. 1980; Kuehne and Barbour 1983; Page 1983; Burr and Warren 1986; Starnes and Etnier 1986) indicates a fish assemblage of 189 species for the Cumberland River basin (Table 4). This total includes several recognized but as yet undescribed species. Thirty-one species can be considered Cumberland regional endemics, 12 of which are restricted to the Cumberland River system. Most of the endemic species are members of the genera *Etheostoma* and *Notropis*. A record for *E. jessiae* (Jordan and Brayton 1878) was presented for the Stones River in Kuehne and Barbour (1983); however, identity

of that population was suspected to be incorrect and was not listed by Page (1983). Eleven species have been introduced into the basin.

LIFE HISTORIES

As documented by the early studies on life histories (e.g., Lefevre and Curtis 1910a,b, 1912; Young 1911; Howard 1914c, 1915, 1922; Arey 1921; Coker et al. 1921), reproduction of North American mussels is a rather complicated process. Following gametogenesis, ova are discharged into the suprabranchial chamber of the female and are fertilized by exogenous sperm which have entered the pallial cavity suspended in the incurrent water flow. Resulting zygotes are deposited in the lumina of marsupial gills and undergo early cleavage stages. Often the embryos are embedded in a secreted, acellular matrix. Development proceeds to a bivalved larval stage, the glochidium. Glochidia may be retained in the marsupia for either a short or extended period of time. Glochidia of most North American mussels require a period of obligatory parasitism on fish in order to metamorphose into juvenile mussels. Parasitism also is the primary dispersal mechanism for mussels (Surber 1913; Fuller 1974). Although highly dependent on water temperature, the parasitic period typically lasts 2-3 weeks (Young 1911; Howard and Anson 1922; Zale and Neves 1982c) but have been reported to be as long as 237 days (*Margaritifera margaritifera*: Williams et al. 1987) and over 7 months (*Simpsonaias ambigua*: Howard 1915). Following metamorphosis juveniles excyst from the host and become free-living components of the benthic fauna. Age of sexual maturation is variable among species but usually requires several years of growth (1-9 years: Smith 1979; Zale and Neves 1982a; personal observations).

Gametogenic cycles have been examined for relatively few mussel species (Zale and Neves 1982a); however, at least 13 of these species are found within the Cumberland River basin (Table 3). Based on seasonal occurrence of gravid individuals and histological examination of gonads, *Cumberlandia monodonta* appears to exhibit a biannual reproductive cycle with spawning periods in late April/early May and late October (Gordon and Smith, in press). Although not conclusively demonstrated to be a consistent trait for all populations, biannual reproduction in *C. monodonta* is referable to a tachytictic (see below) response. Howard (1915) previously had speculated on the possibility of biannual reproduction in *C. monodonta* and *Megalonaias nervosa*. *Anodonta imbecillis* also may produce multiple broods per year (Allen 1924; W.R. Hoeh; pers. comm.; L.M. Koch, Missouri Department of Conservation; pers. comm.). The rest of the examined species followed annual cycles, although with some temporal variation (Table 5). In general, ovulation occurred over a relatively short period, with release of sperm extending for a corresponding but slightly longer time. Populations of some lampsiline species may be highly synchronized and complete ovulation in only a few days (e.g., *Villosa* spp: Zale and Neves 1982a). The more primitive amblemines--e.g., *Quadrula cylindrica* (Yeager and Neves 1986), *Amblema plicata* (Holland-Bartels and Kammer, in press)--and pleurobemines such as *Pleurobema oviforme* (Weaver 1981) may spawn over a period of about 6 weeks to 2 months.

Other histological studies of gonadal tissue found that hermaphroditic individuals may be present in some species. Although hermaphroditism is the predominant condition in a few species, including two known from the Cumberland River system (Anodonta imbecillis and Toxolasma parvum: van der Schalie 1966), the condition is considered to be rare in North American mussels (van der Schalie 1970; Kat 1983c). Out of 111 species/morphs examined, van der Schalie (1970), Heard (1975, 1979), Weaver (1981), and Zale and Neves (1982a) found occasional hermaphrodites in only 30 taxa. Nineteen of the occasional hermaphroditic species occur within the Cumberland River basin (Table 4). The extent of self-fertilization apparently has not been examined. Circumstantial evidence for protandry among freshwater mussels has been presented by Bloomer (1934) and Downing, et al. (1989), but this condition has yet to conclusively be demonstrated in unionoids (see Heard 1975).

With respect to reproductive biology, North American mussels generally have been classified as tachytictic (short-term breeder) or bradytictic (long-term breeder) (Ortmann 1911; also see Lefevre and Curtis 1912). In a seasonal context, corresponding species also have been referred to as summer and winter breeders, respectively (Sterki 1895; Ortmann 1911). Although Lefevre and Curtis (1912) considered Ortmann's (1911) terminology to be awkward, the use of tachytictic and bradytictic has persisted in the literature. However, "breeding" may be interpreted to encompass the entire reproductive process or may be restricted to be synonymous with just the period of spawning (i.e., release of gametes: see Zale and Neves 1982c). In the restricted sense, species such as Amblema plicata and Villosa vanuxemii could be considered to represent bradytictic and tachytictic species, respectively, rather than vice versa. The original usage of tachytictic and bradytictic primarily was in a descriptive context relative to the length of time that embryos and glochidia were held or brooded within the marsupial demibranchs. Reference to species as brooders rather than tachytictic or bradytictic "breeders," respectively, would be a closer representation of Ortmann's (1911) original intent (also see Ortmann 1909; Lefevre and Curtis 1912).

Brooding periodicity has been interpreted as a significant evolutionary factor in unionoid phylogenies (e.g., Ortmann 1911; Heard and Guckert 1970; Heard 1974). Generally, the so-called tachytictic condition has been considered to be a pleisiotypic trait; whereas, bradytixis was characterized as a feature of more advanced taxa. Smith (1978) and Gordon and Smith (in press) noted variability in periods of gravidity within the most morphologically primitive unionoid group (Margaritiferidae), but all examined species appeared to be short-term brooders. Likewise, other apparently primitive taxa (e.g., Amblema, Pleurobema) generally have been classified as "tachytictic"; the more advanced Anodontinae and Lampsilinae are considered to be "bradytictic" (van der Schalie 1938).

Generalizations are not without exceptions. Among the more primitive taxa, Howard (1915) and Utterback (1915-1916) found gravid Megalonaias nervosa (as heros Say 1829) with various developmental stages of glochidia during fall and winter months, respectively. Howard (1915-1916) noted that the temporal difference between his and Utterback's (1915) observations probably were due to a latitudinal effect on climate. Although Heard and Guckert (1970) and Heard (1974) listed Megalonaias as "bradytictic," Lefevre and Curtis (1910b), Howard

(1915), and Utterback (1915-1916) considered M. nervosa to be a "tachytictic" form temporally shifted to spawn during cooler seasons--the so-called winter tachytictic of Heard (1975). Lefevre and Curtis (1912), and Howard (1915) additionally speculated on the possible production of two broods per year. Similarly, Heard and Guckert (1970) indicated that several species of Elliptio (sometimes, classified as Popenaias), a genus generally considered to be "tachytictic," were long-term brooders; however, Ortmann (1912) postulated that one of these species (E. popeii [Lea 1857]) was "winter tachytictic."

Although more advanced, the Lampsilinae are purported to be long-term brooders, the relatively primitive Obliquaria reflexa has been recognized short-term brooder (Lefevre and Curtis 1912). Some Michigan populations of Toxolasma lividum (= glans Lea 1834) and Villosa fabalis (Lea 1831) typically are short-term brooders but also may produce multiple broods per year (W.R. Hoeh, pers. comm.). Reproductive variability also has been observed in Anodontinae. Anodonta grandis, may be a long-term (e.g., van der Schalie 1938; as hallenbeckii in Heard 1975) or short-term brooder (Penn 1939; Lewis 1985). Reproduction in A. imbecillis can be typically "bradytictic" (Heard 1975) but may be similar to that of V. fabalis with multiple broods per year (Allen 1924; W.R. Hoeh; 1 comm. Koch, pers. comm.). Anodonta imbecillis also can function as a "tachytictic" form with a rapid succession of broods during warm seasons and then shift to "bradytictic" behavior during colder months (W.R. Hoeh, pers. comm.). These observations probably explain why A. imbecillis has been reported gravid at all times of the year (see Heard 1975). Heard (1975) determined that A. couperiana Lea 1842, and A. gibbosa Say 1824, were "winter tachytictic" species. Similar temporal variability may be present in Alasmidonta (personal observations).

These data indicate that previous, generalized interpretations of reproductive behavior and periodicity have been overly broad. Heard (1974) noted that at the subfamilial level both incubatory responses could be found among representative species. Some mussels conform well to the generalizations (e.g., Villosa: Zale and Neves 1982a; Amblema: Holland-Bartels and Kammer, in press); however, considerable intra- and interspecific variation exists.

In the Cumberland River basin, the only information on mussel reproduction appears to be occasional references noting the collection of gravid specimens (e.g., Ortmann 1912; Wilson and Clark 1914). Although there are few definitive accounts pertaining to reproduction of Cumberland River populations, data on periods of gravidity for indigenous mussels are available from other geographical regions (Table 7). Data are unavailable for some species (e.g., Epioblasma lewisi, Plethobasus cicatricosus) and are incomplete for others (e.g., Dromus dromas, Obovaria retusa); however, presumed behavior may be inferred from the phylogenetic position of the particular genus (see Heard and Guckert 1970; Bogan and Parmalee 1983). This compilation does not consider temporal incongruities due to latitudinal variations or behavioral modifications.

For short-term brooders, reported periods of gravidity generally represented those of populations rather than individual mussels, which may be considerably shorter (Ortmann 1911). The initiation of spawning (i.e., release of gametes) in long-term brooders typically occurs from late July into September depending on species and latitude. Ortmann (1911) observed that some of the more

advanced lampsilines (e.g., Lampsilis cardia) may retain glochidia until after the next spawning sequence. With respect to the highly synchronized and temporally restricted periods of gamete release exhibited by species in advanced lampsiline genera (e.g., Medionidus, Villosa, Lampsilis: see Zale and Neves 1982a), females still brooding the previous season's glochidia during a spawning interval physically would not appear capable of active participation in that event. Without some adaptation for sperm storage, this would imply that some individuals within a population may not breed every year.

Embryos develop into glochidia within the marsupial demibranchs (gills) of the female (see Lillie 1895). In the Margaritiferidae and Ambleminae, the marsupia typically incorporate all four gills (tetragenous marsupia). Although occasional individuals do not utilize all demibranchs (Quadrula cylindrica: Yeager and Neves 1986), this is not the typical condition and has been attributed in particular instances to the rapidity with which some species will abort marsupial contents when disturbed (Lefevre and Curtis 1912). The other North American unionoids are ectobranchous brooders and either the entire outer demibranchs (e.g., Pleurobema, Anodonta, Alasmidonta) or variously modified sections of their distal margins (Ptychobranchus, Cyprogenia, Lampsilis) are marsupial. Several weeks are required for the development of fully formed glochidia (Lillie 1895; Ortmann 1911; Lefevre and Curtis 1912; Howard 1914c; Zale and Neves 1982a; Yeager and Neves 1986). Glochidia of short-term brooders are released soon thereafter but may be retained within the marsupia of long-term brooders until the following spring, summer, or even into the next reproductive season (Ortmann 1911).

While in the marsupium, embryos and larvae often are imbedded in a gelatinous matrix which is secreted by specialized epithelial tissue (Lefevre and Curtis 1910b, 1912). Lefevre and Curtis (1910b) observed considerable interspecific variability in the amount of this material secreted and questioned if its secretion was common to all species (also see Lefevre and Curtis 1912). Smith (1976) noted that matrix was secreted by Margartifera margaritifera (Linne 1758) only after glochidia were fully developed, but Gordon and Smith (in press) found it in the marsupial lumina of Cumberlandia monodonta with the earliest embryonic cleavage stages. The matrix/larval mass generally forms a relatively rigid structure (the conglutinate), which reflects the shape of the watertubes in the marsupial gill. The consistency of conglutinates varies interspecifically from a slurry-like, amorphous ooze in margaritiferids and some anodontines (Lefevre and Curtis 1912; Smith 1976; personal observations) to quite cohesive structures in Obliquaria, Cyprogenia, and Dromus (Lefevre and Curtis 1912; Chamberlain 1934; Ortmann 1912; respectively). The volume of matrix apparently decreases during the brooding period and may be absent when glochidia are released (Lefevre and Curtis 1910b, 1912; Smith 1976).

By the time glochidia develop, the limited yolk content of the embryo apparently has been depleted. It seems improbable that glochidia, particularly those of long-term brooders, could survive the remainder of the brooding period without some sort of energetic input. Lefevre and Curtis (1910b) speculated that glochidia ingested the "leucocytes" (i.e., amoebocytes) that were found in great profusion in the marsupial gills; however, the matrix may serve as an extra-cellular nutrient source. Although generally considered to have structural functions (Lefevre and Curtis 191ob; Smith 1976), the transitory nature of matrix

and the ability of freshwater bivalves to absorb dissolved nutrients (Churchill 1915, 1916; Efford and Tsumura 1973) suggests consumption by glochidia.

The release of glochidia occurs in two ways: discharge of conglutinal masses through the anal siphon, and eruption through orifices in the distal extremities of the distended marsupial water-tubes (Ortmann 1910, 1911). Although data are lacking for some taxa, the former method appears to be typical for more primitive taxa but is replaced by the latter in more advanced genera within the Lampsilinae. In species that discharge through the anal siphon, glochidia may be expelled individually or as an aggregate within the conglutinate (Ortmann 1910, 1911). Relatively primitive ectobranchs (e.g., Cyclonaias, Pleurobema, Elliptio) and the lampsiline Cyprogenia also release their glochidia in this manner (Ortmann 1910, 1911; Lefevre and Curtis 1912; Chamberlain 1934). Other lampsiline taxa have been reported to discharge conglutinates through the anal siphon (e.g., Lea 1859); however, these observations apparently were made on disturbed mussels and may not represent necessarily natural release of infective glochidia. Many mussels (including lampsilines) are rather sensitive and gravid individuals will abort marsupial contents via the anal siphon if disturbed (Lefevre and Curtis 1912; Howard 1915; Chamberlain 1934; Gordon and Smith, in press). Although conglutinates of Ptychobranchus are expelled intact; most species of the Lampsilinae discharge rather loose masses of glochidia (Ortmann 1910, 1911; Lefevre and Curtis 1912).

Most glochidial infestations probably result from fortuitous contact with fish feeding in the vicinity of gravid mussels (Howard 1914c, 1951). Various structures and/or behavioral adaptations appear to have evolved secondarily to enhance chances for successful parasitism. Many gravid mussels will emerge from the substrate to release glochidia. Since discharge of glochidia in some species may be induced by tactile stimulation (see above), such postures apparently increase exposure to potential hosts. Glochidia in other species are suspended in extruded mucal stranus which may come in contact with or be ingested by a host.

Ortmann (1911) observed foraging fish to actively selected discharged conglutinates of Plethobasus cyphyus. Similarly, Neves and Widlak (1988) found that the release of conglutinates could elicit a feeding response in fish. In some species, these structures may mimic aquatic invertebrates in appearance and can be quite conspicuous with white, pink, or red pigmentation. Conglutinates of Ptychobranchus subtentum resemble nymphs of aquatic insects (personal observation), while those of Cyprogenic aberti look like oligochaetes (Chamberlain 1934). Upon ingestion by fish, loosely organized masses readily fall apart within the buccal cavity; however, more consolidated conglutinates (e.g., Obliquaria, Cyprogenia, Dromus) probably must be broken apart by physical manipulation (e.g., action of the pharyngeal teeth). Free glochidia would then be able to attach to gill surfaces. Neves and Widlak (1988) also noted a high frequency for glochidial parasitism among drift-feeding fish (e.g., darters with terminal mouths) following peak densities of glochidia in stream drift.

Although usually unmodified in most mussels, the mantle margin anteroventrad to the branchial siphon in more advanced genera (e.g., Toxolasma, Ligumia, Villosa, Lampsilis) variously is supplemented with papillae and flap-like structures. This region in Epioblasma is compartmentalized somewhat to

accommodate the swollen marsupia, resulting in the evolution of major modifications in the shape of female shells. Prior to glochidial release, the marsupia are extruded between the modified mantle margins which will often exhibit rhythmic, pulsating contractions (Ortmann 1911; Grier 1926b; Welsh 1933, 1969; Kraemer 1970). At this time, tactile stimulation of the marsupia will cause the discharge of glochidia. Although the function of so-called "flapping-behavior" has been contested (see Kraemer 1970), morphology and movement of these structures, the tactile sensitivity of marsupia, and observation of mutilated (i.e., bitten) flaps strongly suggests a mechanism or "lure" for attracting potential glochidial hosts (personal observations; see also Kirtland 1851; Ortmann 1911; Wilson and Clark 1912a; Utterback 1915-1916; Coker et al. 1921; Baker 1928; Howard and Anson 1922; Welsh 1933, 1969).

Periodicity of glochidial release typically has been linked to the generalized concepts of brooding behavior: "tachytictic" mussels release during the summer, "bradytictic" species release during late spring and early summer (Ortmann 1911; Lefevre and Curtis 1912). However, Surber (1913) noted autumnal parasitism of fish by glochidia of long-term brooders. Within a multi-species mussel community, Neves and Widlak (1988) found that short-term brooders discharged glochidia only from June through mid-August but that long-term brooding lampsilines released glochidia non-synchronously throughout the year. Peak abundance of released lampsiline glochidia was during June and July. Kitchel (1985) observed that glochidial discharge was most frequent between 1000 and 1500 hours. Zale and Neves (1982a) also reported release of glochidia by lampsilines throughout the year but recorded considerable temporal variation among species.

Aspects of glochidial morphology, encystment and excystment, and behavior have been discussed throughout the literature on mussel reproductive biology (e.g., Lefevre and Curtis 1910a, 1910b, 1912; Coker and Surber 1911; Young 1911; Surber 1912, 1913, 1915; Howard 1914c; Arey 1921, 1924, 1932a, 1932b; Coker et al. 1921; Howard and Anson 1922; Heard and Hendrix 1964; Waller et al. 1988). North American unionoids exhibit four general glochidial shapes (Table 8; see Surber 1912, 1915; Smith 1976). Glochidia of the Anodontinae typically are considered to be fin parasites, while those of the other groups attach to gill filaments (Lefevre and Curtis 1910b, 1912). Although field observations support these generalizations (e.g., Lefevre and Curtis 1910b, 1912; Surber 1913; Howard 1914c; Neves and Widlak 1988), the region of a fish parasitized may be partially a function of behavior rather than solely due to morphology. Glochidia or conglutinates that have been ingested presumably would tend to attach to tissues such as gills. Haphazard physical contact would result in parasitism of outer surfaces. Amblemid-type glochidia have been recorded from fins and gill opercula (Lefevre and Curtis 1910b, 1912; Howard 1914c, Neves and Widlak 1988). Anodontine glochidia occasionally have been reported on gill filaments (e.g., Young 1911; d'Eliscu 1972; Zale and Neves 1982b).

Although larvae of some mussels appear to be capable of metamorphosis without parasitism (Lefevre and Curtis 1911, 1912; Howard 1914d; Parodiz and Bonetto 1963), glochidia generally have been considered obligate parasites on aquatic poikilothermic vertebrates during the transformation to the juvenile stage (Leydig 1866; Lefevre and Curtis 1910b; Kat 1984). Fish typically have been identified as the glochidial hosts of most species, but a few cases

(Eurasian) of parasitism on Amphibia and a questionable record of glochidia on a leech have been reported (Faussek 1901; Seshaiya 1941, 1969). Howard (1915, 1951) found only one North American mussel (Simpsonaias ambigua) to successfully metamorphose on an organism other than a fish (Amphibia: Necturus maculosus), although he also observed an apparently unsuccessful infestation of Megalonaias nervosa glochidia on Necturus. The role of Amphibia as glochidial hosts for North American species has not been examined extensively but may warrant further study.

Glochidia of Anodonta imbecillis, Strophitus undulatus, and Obliquaria reflexa have been alleged to metamorphose into juvenile mussels "without a parasitic stage (Lefevre and Curtis 1911, 1912; Howard 1914c, 1914d, 1915; Utterback 1915-1916; Clark and Stein 1921; Allen 1924); however, the case for O. reflexa was founded on conjecture due to the inability to identify a glochidial host. Subsequently, fish hosts were identified for A. imbecillis and S. undulatus (Howard 1914c; Ellis and Keim 1918; Tucker 1927; Baker 1928; Clarke and Berg 1959; Parker et al. 1980; Trdan and Hoeh 1982), suggesting that these species may be facultatively non-parasitic. Metamorphosis without parasitism has been induced with physiological media under laboratory conditions (Ellis and Ellis 1926; Isom and Hudson 1982).

Identification of host species for glochidia has been difficult because of often narrow host-specificity displayed by some mussel species (e.g., Lefevre and Curtis 1912; Howard 1914a, 1914c; Coker et al. 1921; Zale and Neves 1982c). Despite the considerable early work on mussel reproduction and propagation by the Bureau of Fisheries (see Introduction), Fuller (1974) estimated that glochidial hosts had been identified for only about one-fifth of the North American unionoids. Subsequent studies have identified hosts for additional species (e.g., Trdan 1981; Trdan and Hoeh 1982; Zale and Neves 1982b, 1982c; Sylvester et al. 1984; Kitchel 1985; Neves et al. 1985; Hill 1986; Waller et al. 1986; Yeager and Neves 1986; Holland-Bartels and Waller 1987) but probably have not increased significantly the estimated proportion of species with known hosts. In a few instances, the only known hosts are introduced exotics used in laboratory investigations (e.g., Chamberlain 1934; Tompa 1979). Obviously, data on glochidial hosts is less than definitive (Trdan and Hoeh 1982; also see below).

Of the mussels indigenous to the Cumberland River, glochidial hosts have been identified for 45 species or approximately one half of the historical fauna. However, 21% of the host fish have not been reported from the Cumberland system, including the only known host for Obovaria olivaria. Sixty-one species of fish (33% of the historical fauna) and the amphibian Necturus maculosus are recognized as hosts for 44 species of mussels within the basin (Table 9). Short-term brooding species and the generally long-term brooding Anodontinae utilize fish hosts from a wide range of families with no apparent affinity for any particular taxonomic group (Table 10). The more advanced Lampsilines primarily parasitize perciform families. Previous investigations have noted similar relationships (e.g., Howard 1914c; Coker et al. 1921; Stern and Fedler 1978; Zale and Neves 1982c) and Fuller (1974) observed that approximately half of the mussels with known glochidial hosts parasitize centrarchids. Neves and Widlak (1988) also found a strong prevalence for lampsiline species to utilize perciforms as hosts; however, their data indicated an absolute correlation between short-term brooders

(presented as Ambleminae) and the Cyprinidae. Frequency of glochidial parasitization within a fish assemblage generally appears to be less than 20%; however, frequency may be quite variable among species (Trdan 1981; Zale and Neves 1982c; Neves and Widlak 1988). Neves and Widlak (1988) noted that the low prevalence of infestations and low densities of glochidia on parasitized fish reflected the relative inefficiency of unionoid reproduction.

Following parasitism by glochidia, fish have been reported to develop an immunological response which inhibits or prevents later infestations (Reuling 1919; Arey 1923, 1932c; Meyers et al. 1980). Wilson (1916) found that copepod parasitism of fish could induce a similar response which would prevent subsequent glochidial infestations, and vice versa. However, Young et al. (1987) were able to successfully reinfect previously parasitized fish with margaritiferid glochidia and attain densities of encysted glochidia comparable to prior infestations.

HABITAT UTILIZATION

The need for information pertaining to the ecology of freshwater mussels was expressed in early studies by the Bureau of Fisheries (Lefevre and Curtis 1910b; Isely 1911; Coker et al. 1921). Various publications, primarily faunal surveys, have provided descriptive accounts of general habitats and microhabitat utilization (e.g., Baker 1898, 1928; Call 1900, Scammon 1906; Howard 1914c; Ortmann 1919; Coker et al. 1921; van der Schalie 1938; Clarke and Berg 1959; Murray and Leonard 1962; Parmalee 1967; Pennak 1978; Buchanan 1980; Bogan and Parmalee 1983); however, many of these characterizations are vague, of limited scope, and often present conflicting data (Strayer 1981). The few quantitative ecological investigations usually have considered only microhabitats available within limited areas, and little is known about niche relationships.

The niche has been conceptualized as a n-dimensional hypervolume composed of various resource axes critical to and defining optimal conditions for an organism's survival and successful reproduction (Hutchinson 1957; Pianka 1983). Since optimal conditions rarely are encountered, the actual or realized niche typically will be smaller than the fundamental niche (see Pianka 1983). Along particular resource axes, there usually is a tendency for individuals of a species to aggregate within a relatively narrow range of values. The region where peak values of the various resource axes coincide represents that species' "preferred habitat." Dependent on the number and quality of available microhabitats within an area, a species' realized niche and apparent preferred habitat may vary between sites although remaining within the constraints of the fundamental niche (see Strayer 1981). Most "ecological" studies of unionoids have not considered these attributes. Rather, they have tended to be compilations of general limnological or water quality data and have not attempted to correlate physical, temporal, or trophic parameters with mussel distributions and densities.

Organisms adapted to dynamic environments (e.g., temperate lotic ecosystems) expectably would exhibit rather broad tolerances to the inherent

fluctuations of physical factors (Tevesz and McCall 1979; Strayer 1981; Vannote and Minshall 1982; Gordon 1987a). Although within the range of species-specific utilization, extreme values of some resource parameters may represent marginal habitat at best or even conditions where survival is possible only on a short-term bases. In communities with several similarly adapted species, niche overlap may be considerable and indicative of possible inter-specific competition. Strayer (1981) contended that dispersal, densities, and niche breadth functioned in conjunction with the environmental heterogeneity of streams to minimize competition and niche specialization in unionoid mussels. However, Kat (1982) speculated that density effects could result in competitive interactions for high quality microhabitats. Although Bronmark and Malmqvist (1982) documented resource partitioning and possible interspecific interactions between unionoid species, their observations indicated a lack of competition trophically. In undisturbed systems, environmental conditions rather than competitive exclusion appears to limit the distributions of freshwater mussels (see also Pianka 1983; MacArthur 1972; Vannote and Minshall 1982; Strayer 1983; Vance 1985; Green 1986).

Hypothetically, all factors comprising a niche affect an organism's fitness; however, not all resource axes within the realized niche represent significant discriminators of habitat utilization. Typically, habitat preference has been characterized by only a few dominant factors. Substrate composition and current velocity generally are identified as the most significant resource parameters for freshwater benthos, including mollusks (e.g., Cummins 1962; Harman 1972; Ross and Ultsch 1980; Sickle 1981; Williams 1981; Hawkins et al. 1982; Gordon 1987b; Holland-Bartels and Waller 1987). Other factors commonly examined in studies of habitat preference and occasionally identified as significant predictors of habitat use include depth, temperature, dissolved oxygen, light, chemical components of water and substrate, species interactions, and trophic niche.

As noted above, substrate composition has been considered a primary determining factor for the distribution of mussels among microhabitats (e.g., Coker et al. 1921; Harman 1972; Bronmark and Malmqvist 1982; Stone et al. 1982; Vannote and Minshall 1982; Salmon and Green 1983; Stern 1983; Kitchel 1984, 1985; Sylvester et al. 1984; Holland-Bartels and Waller 1987). However, Fuller (1980) contended that "substrate type rarely is a taxon-specific habitat requirement" and Cvancara (1972) and Porter and Horn (1983) found no correlation between substrate type and the distribution of mussels among lentic habitats. Species-specific responses to substrate type are quite variable (Coker et al. 1921). Some mussels have been reported from fine-particle substrates in large river situations but are found in coarse, rocky bottoms in smaller streams. Other species are more restricted in substrate utilization (Sickle 1981). Sylvester, et al. (1984) found that Lampsilis higginsii would not burrow into coarse substrate, while Holland-Bartels and Waller (1987) noted apparent selectivity for fine to medium sands by this species. Moreover, substrate type can affect growth rates (Kat 1982; Hinch et al. 1986). Basin geomorphology, and its effects on substrate composition, also has been implicated as a controlling factor in the distribution of mussels (Strayer 1983; Vannote and Minshall 1982). Aspects of substrate stability have been addressed in Imlay (1972) and Vannote and Minshall (1982).

Current velocity is another factor considered critical in the distribution of many mussels (Baker 1928). As a predictive parameter for faunal distributions, there is a relatively high correlation between current velocity and substrate composition (Gordon 1987). Due to complexities of flow patterns, effects of current on distributions of benthos have been difficult to quantify (Williams 1981). Many studies have noted the association of mussels with various current velocities (e.g., Ortmann 1919; Baker 1928; Buchanan 1980; Holland-Bartels and Waller 1987). However, some records of mussels from swiftly flowing environments actually represented sheltered microhabitats (see Vannote and Minshall 1982; Neves and Widlak 1987) and conditions in some habitats (e.g., headwaters) may vary seasonally from torrents to intermittent pools with no surface flow. Metabolic rates of benthos (including mussels) increase with increased current velocity (Hynes 1970; Payne and Miller 1987). Distributions of unionoids relative to current velocity in part may represent coevolutionary adaptations with or simply may reflect the habitat utilization of the glochidial host.

There is relatively little information linking depth to the microdistribution of lotic benthos (Williams 1981). Although Stern (1983) examined mussel distributions with respect to depth in large river habitats, most data pertaining to lotic systems are derived primarily from incidental records compiled during faunal surveys (e.g., Coker et al. 1921; Baker 1928; Parmalee 1967; Buchanan 1980). In the upper Mississippi River basin, depth was determined to be a factor in mussel distributions only because it reflected changes in substrate composition and current velocity (Stern 1983). A few studies specifically have examined depth distributions in lakes and reservoirs (e.g., Harman 1972; Cvancara 1972; James 1985). Depending on species, mussels generally occur at depths ranging from a few centimeters to about 7 m (Reigle 1967; Pennak 1978); however, Reigle (1967) and James (1985) reported distributions descending to depths of approximately 30 m. Although preferred depths are quite variable, there is a tendency for densities to decrease and individuals to be stunted with increasing depth. Depth limitations probably are due to interactions with other environmental parameters (e.g., substrate, temperature, dissolved oxygen). Reigle (1967) speculated that distributions at extreme depths were food limited, but most studies have concluded that the limiting factor is low temperature (James 1985). Cvancara (1972) found that distributional limits of mussels corresponded with the summer depth of the metalimnion.

Effects of temperature on mussels have been reviewed by Fuller (1974). Williams (1981) observed that temperature may affect longitudinal and, to a lesser extent, micro-distributions of lotic benthos. As noted above, low temperatures can restrict mussel distributions or cause stunting. Species also exhibit variation in critical thermal maxima (Salbenblatt and Edgar 1964). As with many poikilothermic organisms, activity levels and reproduction are regulated thermally (e.g., Howard and Anson 1922; Grier 1926a). In cool spring-fed runs, mussel fauna often are depauperate and, independent of stream size, consist of a few species typical of headwater areas (personal observations). Hypolimnetic discharges from reservoirs drastically alter the thermal character of rivers. Whereas, relict populations occasionally may persist in affected areas (e.g., Miller et al. 1984), reproduction usually is arrested or, more typically, mussels in the main channel can not tolerate the often extreme thermal fluctuations of summer discharges (Gordon 1982; Ahlstedt 1983, 1984).

Despite Ellis' (1931a) contention that mussels could not survive levels below 5 ppm, Imlay (1971) observed that riffle species required 2.5 ppm of dissolved oxygen for survival at summer temperatures. Other species have been found to tolerate extended exposure to anoxic conditions (Eddy and Cunningham 1934; Imlay 1971). Ellis (1931b) noted that oxygen tensions below 20% of saturation induced inactivity; however, Hiestand (1938) and Lewis (1984) reported relative insensitivity in unionoid respiration rates until oxygen concentrations declined below 1 mg/l. Tolerance to anoxia and insensitivity to declining oxygen tensions would appear adaptive to low oxygen levels sometimes associated with substrates, backwaters, and elevated summer temperatures. Since these adaptations would tend to widen niche breadth, dissolved oxygen would not appear to be a powerful discriminator in microhabitat preference.

Chemical effects on mussels have been reviewed in Fuller (1974) and Havlik and Marking (1987). Most studies have not considered aspects of microhabitat preference but generally have examined larger scale distributions. As examples, Imlay (1973) postulated that dissolved potassium was a critical factor in mussel occurrence and Cvancara and Harrison (1965) related longitudinal distribution of mussels to oxygen, turbidity, alkalinity, and chloride levels. Adverse effects of increased turbidity and resultant siltation on mussels have been well documented (e.g., Lefevre and Curtis 1912; Ellis 1931a, 1931b, 1936; Chutter 1969; Fuller 1974; Kat 1982; Dennis 1984; Rosenberg and Henschen 1986; Aldridge et al. 1987). Biogeographic variation in shell condition (e.g., shell thickness) also has been examined as a function of dissolved substances (e.g., Green 1972; Cvancara et al. 1978).

Limited data are available on competitive interactions between mussel species (see above). Although there appears to be disagreement over the occurrence of spatial competition, the lack of trophic competition generally has been conceded (Strayer 1981; Bronmark and Malmqvist 1982; Kat 1982). Unionoids have been reported to ingest microorganisms, meiofauna, zooplankton, various forms of algae, organic detritus, and some inorganic material (Wilson and Clark 1912c; Allen 1914, 1921; Evermann and Clark 1918; Coker et al. 1921; Churchill and Lewis 1924; Read and Oliver 1953). Also, direct absorption of nutrients in solution has been observed in mussels (Churchill 1915, 1916). Baker (1928) and Fuller (1974) concluded that detritus was the primary food stuff; however, Fuller (1974) also listed "animal plankters" as a major trophic input. Both disclaimed the importance of algae, particularly diatoms, in the energy budget of mussels. James (1987) determined that sources of primary production accounted for less than 5% of a mussel population's carbon requirements; whereas, allochthonous material (detritus) represented the primary energy source. James' conclusions correlate well with observed mussel/detritus associations (Baker 1928; personal observations). Trophic responses and microdistributions of mussels (e.g., subsurface occurrence of <u>Pegias fabula</u> and <u>Simpsonaias ambigua</u>, see below; seasonal subsurface occurrence of other species: van Cleave 1940) suggest that feeding adaptations of unionoids may parallel those of the Sphaeriidae (see Burky 1983; Lopez and Holopainen 1987). Although Ortmann (1913b) considered food availability a possible limitation to mussel fitness, the occurrence of detritus and heterotrophy in aquatic systems (see Minshall 1978; James 1987) indicates that trophic energy sources probably do not serve as significant limiting factors (Strayer 1981) but may affect microdistributions (Gordon 1987b).

Many benthic organisms have been found to be photophobic (Williams 1981). Phototactic responses have been observed in mussels (Allen 1923; Baker 1928). Relative to reproduction, mantle flapping behavior appears to be positively correlated to light intensity (Kraemer 1970) and glochidial release usually occurs during daylight periods (Kitchel 1985). However, the full significance of the effects of light on unionoid biology is not readily apparent (also see Imlay 1968).

Although habitat preferences of juvenile mussels have been reported to differ from those of adults (Howard 1914c; DuBois 1981), the distribution and habitat use of juvenile mussels are among the least known aspects of mussel ecology. This dearth of knowledge is due largely to the difficulty in finding juveniles (Coker et al. 1921; Matteson 1955). The initial distribution of young mussels is dependent upon the location of their host when excystment of the metamorphosed juveniles occurs. Redistribution may result from active movement or passive dispersal by water currents. Lefevre and Curtis (1912) suggested that after excystment, juveniles may move aimlessly until they either die or find a suitable habitat. Isely (1911) reported finding 32 juveniles of at least eight species in "fairly swift water" with depths of 30 to 61 cm. Some of Isely's specimens apparently were attached to the gravel substrate by byssal filaments which were strong enough to support the juvenile in rapid currents. Howard (1922) indicated that the habitat of young mussels in the Mississippi River was gravel bars swept clean by the current; however, this broad assertion somewhat contradicts his previous observations (Howard 1914c). In a quantitative study of juvenile mussel habitat, Neves and Widlak (1987) found that densities were greatest behind boulders; however, because such habitat was limited at their study site, the majority of juveniles occurred in riffles and runs.

Characterization of juvenile mussel habitat presently is not possible due to the paucity of available data. In laboratory studies high flow velocities (1.2 m/s) were found to dislodge most newly metamorphosed mussels from silt and sand substrates (Holland-Bartels and Waller 1987), and juvenile metabolic rates rise significantly with increasing current velocities (e.g., Fusconaia ebena: Payne and Miller 1987). Additional experiments are needed to determine whether juveniles have habitat preferences or their distributions are determined more by chance differential survival rates among habitats.

Ecological relationships of most mussel species inhabiting the Cumberland River system are unknown. The majority of habitat information consists of incidental site descriptions compiled during faunal surveys conducted primarily in physiographic regions considerably different from those comprising the Cumberland basin (e.g., Baker 1928). Despite the lack of pertinent regional studies, habitat of each species has been characterized from available published and personal data.

ACCOUNT OF SPECIES[1]

ACTINONAIAS LIGAMENTINA

This species occurs in a variety of habitats from small to large rivers and occasionally reservoirs. It generally is not found in creeks or headwater situations. In small to medium-sized rivers, it tends to be associated with riffles, rocky substrates (occasionally sand), and depths to about 1 m. Often the dominant species in larger rivers, *A. ligamentina* may occupy shallows along banks, riffles, and shoals or occur in pools with depths that may be greater than 4 m. In these latter habitats, little if any preference for substrate type appears to be expressed. Current velocities of 0-3. m/s have been reported for this species (Ortmann 1919; Baker 1928; Buchanan 1980).

ACTINONAIS PECTOROSA

This mussel generally is found in small to medium-sized rivers. It rarely has been encountered in large rivers. *Actinonaias pectorosa* appears to be adapted to riffle areas (in or immediately above them) and occupies sand or hetrogeneous mixtures of substrate types. Occurrences in mud are not common and depths tend to be a meter or less. Current velocities may be moderate to swift.

ALASMIDONTA ATROPURPUREA

This mussel occurs in creeks to medium-sized rivers in the upper Cumberland River basin. It is most common in the smaller stream habitats and may occupy headwater areas. It appears to be most abundant in flats with sand and scattered cobble/boulder material, relatively shallow depths, and slow almost imperceivable currents. This species also inhabits mud, sand, and gravel mixtures and faster currents. Whereas the two subsequent *Alasmidonta* species almost always are buried with only the siphons exposed *A. atropurpurea* may be buried or a third to half of the shell may protrude above the substrate (Call and Parmalee 1982).

ALASMIDONTA MARGINATA

This species is distributed widely in small to large rivers and substrates of mud to gravel usually are preferred. Although it may occur in areas with calm water, *A. marginata* tends to occupy habitats in moderate to swift currents. Specimens have been collected from as deep as 2 m. It occasionally is associated with macrophyte beds (Baker 1928; Clark and Berg 1959; Buchanan 1980).

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[1]Taxa followed by an asterisk are federally listed endangered species.

ALASMIDONTA VIRIDIS

Although specimens occasionally may be found in lentic and medium to large river habitats, *A. viridis* typically is a species of creeks and smaller streams. It often is the only mussel species encountered in extreme headwater areas. It occupies substrates of mud, sand, and gravel in which the shell is buried completely and usually is found in waters of less than 1 m depth. Current velocities tend to be calm to slow, but it also has been reported from swift flowing waters. In lotic habitats, *A. viridis* occurs in riffles, pools, and along banks, particularly in large rivers and may be associated with macrophyte beds (Wilson and Clark 1914; Baker 1928; van der Schalie 1938; Buchanan 1980).

AMBLEMA PLICATA

A widely distributed generalist, this species is found in a considerable array of habitats from creeks to large rivers, lakes, and reservoirs (e.g., Buchanan 1980) and reflects ecophenotypic variation between these environments (Ball 1922). Several names have been applied to these variants (e.g., *costata* Rafinesque 1820, *peruviana* Lamarck 1819, *rariplicata* Lamarck 1819); however, electrophoretic data in Davis and Fuller (1981) indicate that only one of these named forms (*perplicata* Conrad 1841 - Gulf coastal drainages) represents a distinct taxon. *Amblema plicata* has been observed in most substrates (including cracks in bedrock) but exhibits a tendency for coarser substrates in smaller streams. Inhabited depths range to 10 m and current velocities of 0-3.5 m/s have been noted (Baker 1928; Buchanan 1980; personal observations).

ANODONTA GRANDIS

Although found in swift flows and rocky substrates, *A. grandis* typically occupies habitats with little or no flow and mud, sand, and gravel substrates. It can be associated with detrital accumulations or macrophyte beds. In addition to lotic situations, it commonly inhabits ponds, lakes, and reservoirs and probably is now a common species in the Cumberland River due to the extensive impoundments. Its habitat and geographical ranges and the wide array of glochidia fish hosts utilized indicate that *A. grandis* is quite adaptable. It has been recovered from depths as great as 31 m (Ortmann 1919; Baker 1928; van der Schalie 1938; Parmalee 1967; Reigle 1967; Clarke 1973; Buchanan 1980).

ANODONTA IMBECILLIS

This mussel is rather ubiquitous and may be found in most types of freshwater habitats. Although typically most abundant in calm waters with fine particle substrates, *A. imbecillis* also occurs in fast-flowing, high gradient streams with cobble/boulder bottoms. It may occur in areas of detrital deposition or "muck," in pools, large rivers, or along mud banks near the edge of the water. It usually inhabits depths down to 1.5 m (Ortmann 1919; van der Schalie 1938; Parmalee 1967; Buchanan 1980). *Anodonta imbecillis* is another species that has become more common due to the impoundment of the Cumberland River.

ANODONTA SUBORBICULATA

This species tends to be associated with larger rivers and typically inhabits sloughs, oxbows, and backwaters with little if any noticeable current. It has been found in shallow to deep water situations and usually in mud or sand substrates. Although once considered rare, A. suborbiculata appears advantageously to be colonizing reservoirs and, in particular, sheltered inlets (personal observations).

ANODONTOIDES FERUSSACIANUS

This mussel primarily occurs in creeks to small rivers, occasionally in medium-sized rivers and lakes. Water depths in lotic habitats usually are less than 1 m; however, it may be found as deep as 2 m in lakes. Substrates range from clay and mud to gravel with scattered cobble. It typically inhabits calm to slow-moving water in pools and flats. This species rarely has been reported from fast flowing stream sections. It also occurs in headwaters (Ortmann 1919; Baker 1928; van der Schalie 1938; Parmalee 1967; Clarke 1973; Buchanan 1980).

ARCIDENS CONFRAGOSUS

A species typical of large lowland rivers with sand and mud bottoms, A. confragosus also can occur in medium-sized rivers with coarser substrates. It usually has been found in waters less than a meter in depth but also has been listed from deep water habitats. Current velocities from standing to swift have been reported. Arcidens confragosus sometimes inhabits backwater sloughs (Goodrich and van der Schalie 1944; Buchanan 1980; Clarke 1981).

CUMBERLANDIA MONODONTA

This mussel inhabits medium to large rivers and typically is embedded in a vertical position in mud, sand, or gravel substrates. Often, the shell is buried almost completely and easily may be overlooked. Preferred microhabitats are associated with, but not necessarily in, stream sections with swift currents and may include slackwater areas around macrophyte beds, between or behind boulders, or underneath large flat rocks (Baker 1928; Stansbery 1966; LaRocque 1967; Bogan and Parmalee 1983; Ahlstedt 1984). Current velocities of 6-18 cm/s have been measured in these habitats. This species has been collected from as deep as 3.7 m but generally is found in depths less than 1.1 m (Buchanan 1980). Although depths were not specified, Ahlstedt (1984) recovered live specimens of this mussel from sublotic sections of upper Melton Hill Reservoir (Tennessee River basin). Distributions of C. monodonta tend to be quite aggregated with several often even-aged individuals crowded together in a very small area (Stansbery 1966; Buchanan 1980; personal observation). Such occurrences suggest that glochidia may excyst simultaneously from a host. Specimens found in the Cumberland River below Wolf Creek Dam (Miller et al. 1984) and the Caney Fork River downstream from Center Hill Dam indicate that C. monodonta can tolerate hypolmnetic reservoir discharges which are often detrimental to mussels (Gordon 1982). Small, presumably young specimens of C. monodonta reported by Ahlstedt

(1984) and recovered from the lower Caney Fork indicated that it may be able to remain reproductively active in some areas receiving hypolimnetic discharge.

CYPROGENIA STEGARIA

In medium-sized rivers, this mussel occurs in coarse sand/gravel/cobble substrates, moderate to swift currents, and depths to about 1 m. It apparently is more common in large-river habitats that are relatively deep and have gravelly bottoms and moderate currents. A few populations have survived inundation and persist in sublotic zones of reservoirs. Their reproductive status is unknown (Wilson and Clarke 1914; Ortmann 1919; Parmalee 1967; Parmalee et al. 1980).

CYCLONAIAS TUBERCULATA

Ecophenotypic variation within this species is expressed by the compressed, nominate form of small to medium-sized rivers and an inflated, large river morph (granifera Lea 1838, of older publications; see Wilson and Clark 1914). While usually associated with riffles, coarse-particle substrates, swift currents, and depths of less than 1 m in smaller rivers, it also may be found in mud along banks or adjacent to macrophyte beds. In large rivers, C. tuberculata may colonize areas with mud, sand, or gravel substrates and depths of <3 m. Occasionally, lentic environments are inhabited (Baker 1898; Ortmann 1919; Parmalee 1967; Buchanan 1980).

DROMUS DROMAS*

This species occupied riffles and shoals with sand/gravel/cobble substrates, shallow water (1 m or less), and moderate to swift currents. It tended to be found in these areas in medium to large rivers (Bogan and Parmalee 1983). Wilson and Clark (1914) and Ortmann (1920) noted ecophenotypic variation between the compressed, upstream form (caperatus Lea 1845) and typical D. dromas of large rivers. Relict populations have been found in portions of impoundments that receive flowing water at depths greater than 6 m (Tennessee Valley Authority 1976; Parmalee et al. 1980; Ahlstedt 1984). Impounded populations do not appear capable of reproduction (U.S. Fish and Wildlife Service 1984c).

ELLIPSARIA LINEOLATA

This species may be found in medium-sized streams but is more common in large rivers. Although generally associated with riffles and shoals, it can occur at depths greater than 2 m. Substrates of mud, sand, gravel, and occasionally cobble are preferred. Current velocities between 0 and 50 cm/s are typical (Ortmann 1919; Baker 1928; Parmalee 1967; Buchanan 1980). Ellipsaria apparently is quite intolerant of siltation and pollution (Parmalee 1967).

ELLIPTIO CRASSIDENS

Although not usually considered to show ecophenotypic changes, E. crassidens from the upper Cumberland River is "short and chunk" in comparison to the form generally encountered (Wilson and Clark 1914). It has been classified as a large river species but occasionally may be found in the lower sections of medium-sized tributaries. This species has been reported from gravel/cobble/boulder substrate assemblages in rapidly flowing water and at depths that may exceed 2 m. Apparently, it also may be found in mixtures of mud, sand, and gravel and can tolerate some reservoir environments (Call 1900; Ortmann 1919; Baker 1928; Parmalee 1967).

ELLIPTIO DILATATUS

This species is fairly ubiquitous in distribution. Elliptio dilatatus is found in small to medium-sized rivers, may be locally common in large rivers, but also inhabits lentic environments. It exhibits no apparent preference for any particular substrate type and has been collected from depths down to 3 m (Ortmann 1919; Baker 1928; Parmalee 1967).

EPIOBLASMA ARCAEFORMIS (Presumed Extinct)

This species was distributed through medium to large rivers in the vicinity of riffles and shoals (Ortmann 1918).

EPIOBLASMA BIEMARGINATA* (Presumed Extinct)

Distributional records in Johnson (1978) are from medium to large rivers. It evidently was a riffle species and inhabited shallow areas with moderate to fast-moving water (Bogan and Parmalee 1983).

EPIOBLASMA BREVIDENS

This mussel is associated with riffle systems in medium-sized and, more rarely, large rivers. Substrates range from coarse sand to mixtures of gravel, cobble, and boulder. Depths tend to be less than 1 m (Wilson and Clark 1914; Bogan and Parmalee 1983).

EPIOBLASMA CAPSAEFORMIS

This species is found in small to large rivers. Currents vary from moderate to quite swift and substrates tend to be combinations of sand to boulder sized particles (rarely mud). It may be associated with Justicia americana beds bordering the main channel of the riffle (Ortmann 1924a).

EPIOBLASMA FLEXUOSA (Presumed Extinct)

Data is lacking for this species. *Epioblasma flexuosa* apparently preferred deep water habitats with mud to sand bottoms in large rivers (Bogan and Parmalee 1983).

EPIOBLASMA FLORENTINA* (Presumed Extinct)

Apparently a species of medium to large river habitats, *E. florentina* is assumed to have inhabited riffles and shoals with sand to cobble substrates and moderate to swift currents (Neel and Allen 1964; Bogan and Parmalee 1983; inferences based on locality records in Wilson and Clark 1914, and, in part, Johnson 1978).

EPIOBLASMA HAYSIANA (Presumed Extinct)

Distributional records indicate that this species occurred in medium to larger and possibly some small river habitats. It apparently occupied sand to cobble substrates and may have preferred cool, high-gradient environments (Bogan and Parmalee 1983; inferences based on locality records in Wilson and Clark 1914, and Johnson 1978).

EPIOBLASMA LENIOR (Presumed Extinct)

This was a species of small to medium-sized rivers with clear, fast flowing water. Preferred substrates were sand and gravel, probably mixed with some cobble and boulder. It was collected from depths of less than 1 m (Bogan and Parmalee 1983).

EPIOBLASMA LEWISI (Presumed Extinct)

This mussel was found in medium to large river habitats. It apparently inhabited shallow riffles presumably with sandy to rocky substrates and substantial currents (Johnson 1978; Bogan and Parmalee 1983).

EPIOBLASMA OBLIQUATA

This mussel was distributed fairly widely in medium to large rivers. Typical of the genus, *E. obliquata* was associated with riffles, substrates of sand to boulder, moderate to swift currents, and shallow to moderate depths (Stansbery 1971; Bogan and Parmalee 1983). A relict population of *E. obliquata* persists in a sublotic zone of Old Hickory Reservoir (Cumberland River) with sand/gravel substrates and depths as great as 10 m (Tennessee Valley Authority 1976; Isom et al. 1979; Parmalee et al. 1980; Bogan and Parmalee 1983).

EPIOBLASMA PERSONATA (Presumed Extinct)

Distributional records in Johnson (1978) indicate that E. personata inhabited medium to large rivers. Following Stansbery's (1971) characterization of habitats for Epioblasma, this species apparently was found in areas of riffle or shoals, sand to rocky substrates, and moderate to swift currents.

EPIOBLASMA STEWARDSONII (Presumed Extinct)

A species found in medium to large rivers (Johnson 1978), it is assumed to have inhabited riffle areas with sandy to rocky substrates and moderate to fast currents.

EPIOBLASMA TORULOSA

This mussel has several recognized forms (torulosa s.s., gubernaculum, rangiana, cincinnatiensis), but it is not clear whether these morphs represent ecophenotypic variation, true subspecies, or a species complex. Epioblasma torulosa inhabits riffle systems with swift currents and stable substrates. Substrate particle-size range from coarse sand to heterogenous mixtures of coarser material and water depths vary from a few cm to about 2 m (Ortmann 1919; Hickman 1937; Parmalee 1967; Johnson 1978).

EPIOBLASMA TRIQUETRA

This species typically is found in riffles and is distributed widely in small to large river habitats. Substrate composition has been listed as combinations of sand, gravel, cobble and boulder. It also has been collected from mud and cracks in bedrock. Bottom current velocities have been reported as moderate to swift and depths of less than 1 m usually are given. Shells tend to be completely buried so that the flattened posterior slope is flush with the substrate (Ortmann 1919; Baker 1928; van der Schalie 1932, 1938; Parmalee 1967; Buchanan 1980). Baker (1928) and van der Schalie (1938) found E. triquetra in mainstream pools with mud to sand substrates and depths to 2.5 m. Additionally, specimens have been collected by Ortmann (1919) from Lake Erie, van der Schalie (1938) in small impoundments, and Tennessee Valley Authority (1976) from a sublotic zone of Old Hickory Reservoir (Cumberland River) at depths of 5-6 m.

EPIOBLASMA TURGIDULA* (Presumed Extinct)

Distributional records in Johnson (1978) indicate that this mussel primarily occurred in small to medium-sized rivers, rarely in large rivers. It is assumed to have been a component of riffle fauna (Bogan and Parmalee 1983).

EPIOBLASMA WALKERI*

This mussel has been confused with E. capsaeformis and often has been considered a small river ecomorph of E. florentina (Ortmann 1918, 1924a). The taxonomic relationship requires rectification. Epioblasma walkeri is distributed through small to medium-sized rivers in riffles with sand, gravel, cobble, and boulder substrates. Current velocities tend to be moderate to swift and depths usually are less than 1 m (Ortmann 1924a; Bogan and Parmalee 1983; U.S. Fish and Wildlife Service 1984f).

FUSCONAIA EBENA

This is a large-river species that occasionally inhabits lower sections of medium-sized tributaries. Although documented to require habitats with swift currents, it also has been observed in moderate currents and areas with almost no perceivable flow. Fusconaia ebena may occur at depths greater than 3 m. Substrate preferences range from mud to gravel, but often it is associated with sand-mud mixtures in deeper habitats (Baker 1928; Parmalee 1967; Buchanan 1980).

FUSCONAIA FLAVA

Fusconaia flava is considered to be a small to medium-sized river form but occasionally inhabits large rivers and lakes (Ortmann 1919, 1920; van der Schalie and van der Schalie 1950). It is fairly general in habitat preferences, being found in a wide variety of substrate types and currents (0-60+ cm/sec). Although usually found in habitats less than 1.5 m deep, flava has been recorded from depths as great as 4 m (Ortmann 1919; Baker 1928; Parmalee 1967; Buchanan 1980).

FUSCONAIA SUBROTUNDA

This mussel typically is found in habitats with strong currents. It may occur in lotic systems ranging from creeks to large rivers and exhibits considerable ecophenotypic variation as a function of river size (shell inflation increases in a downstream direction). Fusconaia subrotunda shows a preference for sand to coarse gravel in smaller streams but also may be found in gravel and cobble in large rivers (Ortmann 1919, 1920).

HEMISTENA LATA

While characterized as a species of small to medium-sized rivers (e.g., Sterki 1907; LaRocque 1967), distributional records exist for H. lata in large rivers (Call 1900; Wilson and Clark 1914; Goodrich and van der Schalie 1944). This species resembles the marine razor clams (e.g., Ensis) in shape and habit; the foot is extended approximately the same length as the shell into the substrate and the shell is completely buried. Only the siphons are visible at the surface. It frequents riffle areas with swift currents and sand, gravel, and cobble substrates (Wilson and Clark 1914; Ahlstedt 1984); however, it also

has been reported from mud and sand in slower flowing waters (Call 1900). Yokley (1972a) found it in gravel substrates in the impounded area downstream from Pickwick Landing Dam, but such populations may not be reproductively viable.

LAMPSILIS ABRUPTA*

This is a large river species but has been found in some medium-sized tributaries. It has been reported from riffles with rocky substrates, strong currents, and depths to about 1 m. Lampsilis abrupta also has been collected from deep water habitats presumably with sand and gravel substrates and slower flows (Ortmann 1919; Parmalee 1967; Bogan and Parmalee 1983). Some relict populations persist at depths down to 5-8 m in sublotic zones of reservoirs (e.g., Yokley 1972a, Tennessee Valley Authority 1976; Hickman and Ahlstedt 1983; U.S. Fish and Wildlife Service 1984e). Some populations in sublotic zones appear to be reproducing (Ahlstedt 1984).

LAMPSILIS CARDIA

This species is one of the best known and is rather ubiquitous in habitat utilization. It has been reported from creeks to large rivers, lakes, and reservoirs. In riffle sections, it often is more common in the flats just above and below rather than in riffles, sometimes is associated with macrophyte beds, and occupies substrate assemblages of sand, gravel, cobble, and boulder. In other habitats, L. cardia has been observed in cracks in bedrock, sand and/or gravel, and mud. It may occur in current velocities from calm to swift and at depths of over 3 m (Ortmann 1919; Baker 1928; van der Schalie 1938; Parmalee 1967; Buchanan 1980).

LAMPSILIS FASCIOLA

This mussel appears to be most common in riffle and flats with sand/gravel/cobble substrates of small to medium-sized rivers. In these areas current velocities tend to vary from slow to moderate. It also has been reported from large rivers. Call (1900) listed it from a few small lakes in northern Indiana; however, van der Schalie (1938) was not able to locate lentic populations. It usually is buried deeply in the substrate (Call 1900; Ortmann 1919; van der Schalie 1938; Parmalee 1967).

LAMPSILIS OVATA

Although generally considered a species of large rivers, L. ovata occasionally is found in medium-sized rivers. It has been reported from riffles with rocky substrates, swift currents, and moderate depths. It also can occur in areas with slower flows, depths greater than 3 m, and sand or gravel substrates (sometimes mud) (Ortmann 1919; Parmalee 1967). Ortmann (1919) discussed the morphological adaptations of L. ovata shell for resisting shear forces of strong current and moving through coarse rocky substrates of riffles.

LAMPSILIS SILIQUOIDEA

This species is rather generalistic in habitat use. It can be found in headwaters to large rivers, lakes, and some reservoirs; however, this rather ubiquitous mussel inhabits only the very most downstream reaches of the Cumberland River. Most substrate types are tolerated, including cracks in bedrock, and *L. siliquoidea* has been collected from depths exceeding 8 m. It can be found in riffle or pools with current velocities varying from swift-flowing to standing (Ortmann 1919; Baker 1928; Parmalee 1967; Buchanan 1980).

LAMPSILIS TERES

Although present in small and medium-sized rivers with rocky substrates, *L. teres* appears best adapted to larger rivers with fine-particle substrates. It may be found in shallow riffles with considerable flows, relatively deep pools, or backwater sloughs and oxbows. Occasionally, it tolerates sublotic conditions in reservoirs. Two shell forms (possibly ecomorphs) exist: the typical unrayed shell occurs in most occupied habitats; a rayed morph (*fallaciosa* Smith 1899) generally is considered a slough form (Wilson and Clark 1914; Baker 1928; Parmalee 1967; Yokley 1972a; Buchanan 1980). Murray and Leonard (1962) did not observe any apparent preference for sloughs or backwaters by the *fallaciosa* morph or habitat differentiation between the two forms. The taxonomic significance of these two forms remains unresolved.

LASMIGONA COMPLANATA

This mussel has been reported from a wide variety of habitats including creeks, large rivers and lentic areas. Substrate composition appears to be a primary limiting factor in the distribution of this species. It most commonly is found in situations with mud, sand, or small gravel substrates (occasionally with scattered cobble and macrophytes). Water flows vary from calm to swift (>60 cm/s at the bottom) and depths to 2 m have been recorded. In lotic habitats, it has been found in riffles, pools, and backwaters (Ortmann 1919; Baker 1928; van der Schalie 1938; Parmalee 1967; Clarke 1973; Buchanan 1980). *Lasmigona complanata* appears to be sensitive to elevated turbidity (Murray and Leonard 1962).

LASMIGONA COSTATA

Although occasionally encountered in lentic habitats, *L. costata* can be found in creeks (including headwaters) to large rivers. It occurs in all substrate types but exhibits an apparent preference for combinations of gravel and cobble. Current velocities measured at the substrate surface range from calm to swift (over 60 cm/s). Despite a tendency to be associated with shallow riffles, this species may occur at depths greater than 4 m in pools (Ortmann 1919; Buchanan 1980). Murray and Leonard (1962) speculated that *L. costata* may be highly sensitive to elevated turbidity.

LEPTODEA FRAGILIS

Often found in the vicinity of riffles, this thin-shelled mussel inhabits all substrate types except bedrock and a wide range of current velocities. Highest densities are attained in medium to large rivers with mud to sand substrates. Although considered to be an active species (i.e., crawls around alot), it tends to burrow deeply into the substrate and uses its foot as an anchor. It may be quite difficult to dislodge from the bottom. In larger rivers, L. fragilis may be quite common and can inhabit depths over 5 m (Ortmann 1919; Parmalee 1967).

LEPTODEA LEPTODON

Despite a very thin shell, L. leptodon often occurs in shallow riffle areas with substrate assemblages of gravel, cobble, and boulder, occasionally mud or sand. Its adaptations to withstand the physical forces inherent to riffles resemble those of Hemistena lata (e.g., shell completely buried in a vertical position with the foot extended as an anchor). Current velocities range from slow to swift. In large rivers, it tends to occur in mud and sand (Call 1900; Buchanan 1980).

LEXINGTONIA DOLABELLOIDES

This Cumberlandian species inhabits riffle areas in small streams to large rivers. It generally has been found in water depths of <1 m and substrates of coarse sand to heterogenous mixtures of large particle-size. Current velocities tend to be moderate to swift. Lexingtonia dolabelloides exhibits some ecophenotypic variation between headwaters (from conradi) and other environments.

LIGUMIA RECTA

This mussel may be found in a variety of habitats including small to large rivers, lakes, and reservoirs. It often is associated with riffles, medium to swift currents, and substrate assemblages of gravel/cobble/ boulder. It also inhabits soft mud to sand, flats or pools above riffles, and oxbow lakes. In lentic habitats, it also exhibits a wide range of substrate tolerances. Ligumia recta can occur at depths greater than 3 m (Ortmann 1919; Baker 1928; Parmalee 1967; Buchanan 1980).

MEDIONIDUS CONRADICUS

This is a small mussel usually found in creeks to medium-sized rivers. It appears to favor riffles, often with high gradients and fast flows, and substrate assemblages of gravel, cobble, and boulder, or occasionally sand and gravel (DiStefanio 1984). It is not unusual for this species to burrow under large, flat rocks.

MEGALONAIAS NERVOSA

Although typically associated with large rivers, M. nervosa may be found in smaller streams. In large rivers, it usually occurs in fairly deep, quiet water with a mud substrate, occasionally sand or gravel. In other habitats, this mussel can occur between a few centimeters and 2 m in depth and in substrates of mud to heterogenous assemblages of gravel, cobble, and boulder. Current velocities of 0-45 cm/s have been reported (Baker 1928; Murray and Leonard 1962; Parmalee 1967; Buchanan 1980; Oesch 1984). Howard (1914c) observed that juveniles and adults occupied the same habitat.

OBLIQUARIA REFLEXA

Although an occasional inhabitant of smaller rivers (e.g., Parmalee 1967; Gordon 1985), O. reflexa usually is considered a species typical of medium to large rivers (Ortmann 1919; Baker 1928). Several references (e.g., Scammon 1906; Baker 1928) have delineated ecological preferences for this species; however, personal observations follow Call's (1900) assessment that O. reflexa is rather ubiquitous in habitat utilized. It may be found at depths greater than 4 m.

OBOVARIA OLIVARIA

This species tends to favor large river habitats, although it may occur in the lower reaches of some medium-sized tributaries. It usually is found in sand or gravel substrates (rarely mud) and moderate currents. In some tributaries, O. olivaria is associated with shallow riffles or shoals; however, it may occur at depths of over 2 m in large rivers (Ortmann 1919; Baker 1928; Parmalee 1967).

OBOVARIA RETUSA

Typically a large river species, O. retusa has been found in substrates of sand and gravel. It evidently is a species of riffles and shoals and did not frequent habitats deeper than about 1 m (Ortmann 1919; Bogan and Parmalee 1983). Relict populations persist in sublotic zones of some reservoirs but reproduction is not apparent (Parmalee et al. 1980; Parmalee and Klippel 1984).

OBOVARIA SUBROTUNDA

This mussel shows considerable ecophenotypic variation in shell inflation between small and large rivers (Ortmann 1920). It occupies habitats with sand, gravel, and cobble substrates, moderate current, and depths to 2 m. In creeks and smaller rivers, perceivable current may be seasonally absent and mussels will be distributed upstream from riffle (Ortmann 1919; Parmalee 1967).

PEGIAS FABULA*

This is a species of creeks and smaller rivers. While usually associated with high gradients and riffle systems, the situations in which it occurs tend to vary. Although DiStefano (1984) found P. fabula buried in pools with sand and gravel bottoms, most other records are for riffle environments. An apparent preferred habitat is at the immediate head of riffles, but it also has been found in and below riffles. It often has been reported as lying on or only partially embedded in substrates of sand and gravel with scattered cobbles. Its occurrence on the surface may be related seasonally to low-flow conditions; the entire shell may be buried during high-water periods. In other instances, P. fabula has been observed in sand pockets between rocks, wedged between cobbles and boulders, and buried beneath large rocks. The typical almost total absence of shell periostracum suggests that this species commonly may burrow through the substrate. Depths generally have been recorded as less than 30 cm and currents vary from calm to 20 cm/s during low flows (Blankenship 1971; Starnes and Starnes 1980; Starnes and Bogan 1982; Bogan and Parmalee 1983; DiStefano 1984; Ahlstedt 1986a).

PLETHOBASUS CICATRICOSUS*

Distributional records indicate that this species primarily colonized riffle and shoals in large rivers with sand to gravel substrates (Bogan and Parmalee 1983; U.S. Fish and Wildlife Service 1984b).

PLETHOBASUS COOPERIANUS*

Distributional records suggest that P. cooperianus inhabited riffles and shoals with sand to gravel substrates in larger rivers (Bogan and Parmalee 1983). In the Ohio River, Ortmann (1919) found this species associated with "shell-banks", deep water, and steady currents. Miller, et al. (1986) recovered specimens from gravel and cobble substrates at depths of 3 to 6 m. It has been reported from depths as great as 9 m (U.S. Fish and Wildlife Service 1984a).

PLETHOBASUS CYPHYUS

Although occasionally inhabiting medium-sized rivers, this mussel generally has been considered a large-river species. It may be associated with riffles and gravel/cobble substrates but usually has been reported from deep-water situations (>2 m) with slight to swift currents and mud, sand, or gravel bottoms (Ortmann 1919; Baker 1928; Parmalee 1967; Buchanan 1980). Ortmann's (1919) characterization of habitat for P. cyphyus was almost identical to that for P. cooperianus.

PLEUROBEMA CATILLUM

The taxonomic validity of this species is questionable. It has been considered an ecomorph of P. coccineum and P. cordatum. In either case, P.

catillum generally represents a faunal component of riffle systems in medium-sized rivers. It rarely is found in other situations. Substrate preferences are similar to those of P. coccineum. It typically occurs in moderate to swift currents and may be found at depths from a few centimeters to greater than 2 m (Ortmann 1919; Baker 1928).

PLEUROBEMA CLAVUM

A species of smaller rivers, P. clavum tends to be deeply buried in sand and fine gravel substrates (Ortmann 1919). It probably occurs in or immediately above riffles. Goodrich and van der Schalie (1944) observed that this species was adapted particularly to small river environments. Some records of P. clavum from the Cumberland River system actually may be P. oviforme.

PLEUROBEMA COCCINEUM

Generally considered a small river species, P. coccineum usually is deeply buried in heterogenous mixtures of gravel, cobble, and boulder in riffle areas. In larger rivers, it is found in mud, sand, and gravel assemblages and at depths greater than 3 m. It also may occur in shallows on sand or gravel bars. Calm to swift flowing currents (>46 cm/s) have been observed for this species (Ortmann 1919; Baker 1928; van der Schalie and van der Schalie 1950; Buchanan 1980).

PLEUROBEMA CORDATUM

This species primarily inhabits large rivers but occasionally may be found in medium-sized rivers. It also appears tolerant of some reservoir environments. In lotic situations, P. cordatum is found in or immediately above riffles in heterogeneous assemblages of gravel, cobble, and boulder. It also occurs in some habitats with greater depth and substrates of mud/sand/gravel but requires flowing water (Call 1900; Ortmann 1919; Goodrich and van der Schalie 1944; Ahlstedt 1984e).

PLEUROBEMA GIBBERUM

This poorly known species appears to be restricted to creeks and small to medium-sized rivers in the Caney Fork River drainage. It is associated with riffle areas, substrates of sand and gravel with occasional mud and cobble, and relatively shallow depths. It has not been found in deep-water habitats (personal observations).

PLEUROBEMA OVIFORME

Ortmann (1920) described the ecophenotypic variation in shell inflation exhibited by this species with respect to river size. Additionally, there appears to be considerable morphological variation within populations. Pleurobema oviforme has been found in small to large rivers in the vicinity of

riffles and shoals. Occupied substrates tend to be sand/gravel mixtures and occasionally mud. It does not appear to tolerate more than moderate depths. In small rivers, it may be found immediately above riffles or in flats (see Leopold et al. 1964). Although there may be seasonal periods of calm water, this mussel usually occurs in areas of at least moderately flowing water (personal observations).

PLEUROBEMA PLENUM*

Distributional records indicate that *P. plenum* is a large river shoal species, presumably occurring in substrate assemblages of sand, gravel, and cobble (Bogan and Parmalee 1983). It occasionally inhabits medium-sized rivers and has been reported from flats and muddy sand (Ahlstedt 1984; U.S. Fish and Wildlife Service 1984).

PLEUROBEMA RUBRUM

This mussel typically inhabits large rivers but occasionally may be found in medium-sized lotic environments. It may occur in riffles or shoals in relatively shallow water and coarse-particle substrates, along sand bars, or in deep water (>4 m) with mud and sand bottoms. Moderate to swift currents usually are associated with these habitats (Baker 1928; Ahlstedt 1984).

PROPTERA ALATA

Proptera alata is rather generalistic in habitat requirements. It has been found in creeks, small to large rivers, ponds, lakes, and reservoirs. Likewise, it may occur in the full range of substrates (including cracks in bedrock) and calm to swift currents. *Proptera alata* inhabits riffles, shoals, or pool environments. It has been collected from as deep as 8 m (Ortmann 1919; Baker 1928; Buchanan 1980).

PROPTERA CAPAX*

Typical of lowland river habitats with sand, mud, or small gravel substrates and slight to moderate current velocities, *P. capax* is found in large and some medium-sized rivers. It also occurs in side channels and backwaters. *Proptera capax* has been collected from depths of >3 m (Parmalee 1967; Ahlstedt and Jenkinson 1987; Jenkinson and Ahlstedt 1988c; U.S. Fish and Wildlife Service 1989).

PROPTERA OHIENSIS

This species may be found in medium-sized rivers but is more common in large rivers. It also inhabits lakes and can be quite abundant in reservoirs. Substrates range from mud through gravel and calm to swift current velocities have been recorded. *Proptera ohiensis* has been reported from sand bars but also

can occur at considerable depths (Baker 1928; Parmalee 1967; Buchanan 1980). Isely (1925) noted that young mussels are rather active and quickly can burrow into the substrate.

PTYCHOBRANCHUS FASCIOLARIS

This mussel is most common in small to medium-sized rivers, rarely in large rivers. It generally is found in riffles with moderate to swift currents and frequently adjacent to Justicia americana beds. In smaller streams, it may occur in flats immediately above riffles. The shell usually is buried deeply in stable sand and gravel with water depth only to about 1 m. It also reflects these ecological preferences in Lake Erie, the only truly lentic environment in which it has been reported (Ortmann 1919; van der Schalie 1938; Parmalee 1967). Populations may persist in shallower sections of impoundments which still have flowing water environments (Yokley 1972a; Tennessee Valley Authority 1976).

PTYCHOBRANCHUS SUBTENTUM

This species typically is a faunal component of small to medium-sized rivers and often occurs in headwater areas. It tends to be fairly deeply embedded in sand, gravel, and cobble substrates and generally is associated with shallow water and moderate to swift currents (Bogan and Parmalee 1983). This mussel rarely has been found in large rivers and then only in situations with shallow depths, rapidly flowing water, and rocky substrates (e.g., Muscle Shoals, Tennessee River: Ortmann 1925; Morrison 1942).

QUADRULA CYLINDRICA

Two forms of Q. cylindrica occur within the Cumberlandian region. Within that portion of the Tennessee River basin, Q. cylindrica strigillata exhibits ecophenotypic variation in shell inflation and development of pustules with respect to river size. Habitat is characterized for this subspecies in Bogan and Parmalee (1983). These traits are not expressed by populations in the Cumberland River or any other drainage systems. Typical Q. cylindrica occurs in small to large rivers and is associated with moderate to swift currents. In smaller streams, it inhabits bars of gravel and cobble in close proximity to areas with the fastest current. In larger rivers, it also may frequent gravel bars in riffles or may occur in deeper water with sand substrate and moderate flow. It occasionally is found in mud or along the edge of macrophyte beds bordering the channel-side of riffles. Quadrula cylindrica has been recovered from as deep as 3 m (Scammon 1906; Murray and Leonard 1962; Parmalee 1967).

QUADRULA FRAGOSA

Quadrula fragosa is a poorly known species that often has been confused with or synonymized under Q. quadrula. Although Neel (1941) considered Q. fragosa to be rare, Call (1900) indicated that it was relatively common and Wilson and Clark (1914) reported it to be locally abundant at sites in the lower

Cumberland River. Wilson and Clark (1914) did not list Q. quadrula and may have lumped the two species under their Q. fragosa. Illustrations in Baker (1928) also suggest such a lumping for Q. fragosa. Available information on habitat indicates preferences for large to medium-sized rivers, depths that may exceed 2 m, and mud substrates (Ortmann 1924a; Baker 1928).

QUADRULA METANEVRA

This species appears to be most common in medium to large rivers but sometimes is locally abundant in smaller rivers. It most often is found in assemblages of sand, gravel, cobble and boulder. To a lesser extent, it also may occur in mud. Quadrula metanevra has been collected from as deep as 4 m and in calm to swift currents (Baker 1928; Murray and Leonard 1962; Parmalee 1967; Buchanan 1980). Scammon (1906) and Ortmann (1919) considered gravel bars to represent preferred habitat. Baker (1928) observed that juveniles tended to be on gravel bars in water shallower than that of adults.

QUADRULA NODULATA

While usually found in large rivers, Q. nodulata also can occur in medium-sized rivers. This species has been reported from shallow to relatively deep water and in mud, sand, and small gravel substrates (Baker 1928; Parmalee 1967).

QUADRULA PUSTULOSA

This widely distributed mussel exhibits ecophenotypic variation with stream size (Ortmann 1920) but also is quite morphologically variable among some stream systems. It may represent a species complex. Quadrula pustulosa has been collected from creeks to large rivers and occasionally in lake and reservoir situations. There is no apparent preference for a particular substrate type, although like other species, it rarely inhabits areas of shifting sand. Depths range from a few centimeters to 3 m and current velocities of 0-52 cm/s have been reported (Baker 1928; Parmalee 1967; Buchanan 1980). In larger rivers, juveniles usually are found on gravel bars in shallow water (Baker 1928).

QUADRULA QUADRULA

Wilson and Clark (1914) did not list Q. quadrula among species they collected (see Q. fragosa, above); however, recent collecting has yielded only Q. quadrula. It is assumed that these previous records for Q. fragosa probably included misidentified Q. quadrula. Generally considered a large river species, Q. quadrula may be found in some lake and reservoir environments and occasionally in smaller rivers. It typically is absent in creeks and headwater situations. In large rivers and lentic habitats, this mussel often is associated with mud or sand substrates and may occur in deep water (>5 m). Habitats with other substrate types are also occupied and bottom current velocities of calm to moderately swift (45 cm/s) have been reported (Ortmann 1919; Baker 1928; Parmalee

1967; Buchanan 1980). Reservoir construction may have expanded available habitat for Q. quadrula to the detriment of Q. fragosa (see Fuller 1980).

QUADRULA TUBEROSA

This is a Cumberlandian species that is restricted to the upper portion of the basin. It apparently was associated with riffles and heterogenous assemblages of substrate types. Most of its former habitat has been inundated, but some relict populations may persist in sublotic zones of reservoirs (personal observations).

SIMPSONAIAS AMBIGUA

Call (1900) reported S. ambigua from mud and gravel bars but found it to be most abundant under large flat rocks. This mussel rarely is encountered, although it may be quite numerous in very localized areas. Collection records (see Clarke 1985; Harris and Gordon 1988) are available for shallow sections of creeks to large rivers (and one instance of a mill pond: Shimek 1888) with calm to swift mid-depth current velocities. Base substrates range from mud to cobble and boulder; however, the tendency for S. ambigua to be under large flat rocks almost universally has been reported (e.g., Shimek 1888; Call 1900; Howard 1915, 1951; Baker 1928; Buchanan 1980; Clarke 1985). Interestingly, Ortmann (1919) discovered S. ambigua deeply buried in sand and gravel amongst the roots of the emergent macrophyte, Justicia americana. Ortmann's (1919) data indicate that this mussel may be found wherever its glochidial host (Necturus maculosus) typically takes refuge.

STROPHITUS UNDULATUS

This species is distributed widely in creeks (including headwaters) to large rivers and lakes. It may be locally abundant in smaller rivers. Strophitus undulatus has been characterized as a species of calm to slow flowing areas with mud to gravel substrates; however, it is not uncommon in habitats with swift currents (60 cm/sec at bottom) and substrates including cobbles and boulders. Although often found in shallows, S. undulatus tends to occupy relatively deeper sites with increasing stream size. It has been collected from depths as great as 4 m (Ortmann 1919; Baker 1928; van der Schalie 1938; Goodrich and van der Schalie 1944; Parmalee 1967; Clarke 1973; Buchanan 1980).

TOXOLASMA LIVIDUM

This species usually occurs in creeks to medium-sized rivers. It often is the first mussel species encountered in headwater areas. While similar to T. parvum in occupying fine-particle substrates near banks, T. lividum also inhabits sand, gravel, cobble, and/or boulder assemblages in riffles or flats immediately above riffles. It generally occurs at depths <1 m (Call 1900).

TOXOLASMA PARVUM

Although typically considered a species of creeks, small rivers, and ponds, T. parvum also inhabits larger rivers, lakes, and reservoirs. It tends to occur in areas with sluggish to no current (rarely swift), depths of less than 1 m and fine-particle substrates. Occasional specimens have been collected from gravel/cobble substrates. In some ponds, it has been found at depths of several meters. Generally, T. parvum will be completely buried at depths of only a few centimeters and near the bank. It often is associated with mud accumulated around macrophyte beds (Baker 1898, 1928; Buchanan 1980).

TRITOGONIA VERRUCOSA

Tritogonia is distributed widely and inhabits a diverse range of lotic and occasionally lentic habitats. In creeks and smaller rivers, it exhibits a propensity for riffles with bordering macrophyte beds (e.g., Justicia americana) and coarser substrates. Large river habitats tend to have mud or sand bottoms and depths of 3 m or greater. The mussel often is only partially buried at an oblique angle in coarse-particle substrates; whereas, in sand and mud, it usually is buried completely with only the siphons exposed. Bottom current velocities of 0-52 cm/s have been observed for this species. In large rivers, juveniles may be found on sand bars (Scammon 1906; Ortmann 1919; Baker 1928; Parmalee 1967; Buchanan 1980).

TRUNCILLA DONACIFORMIS

This diminutive mussel apparently is adapted to habitats in large rivers and their medium-sized tributaries. It also has been reported from lentic situations. Preferred substrates are mud, sand, and gravel, but these may be mixed with cobble and boulder. Current velocities may range from calm to swift and depths exceeding 2 m have been reported (Parmalee 1967; Buchanan 1980).

TRUNCILLA TRUNCATA

Although occasionally found in creeks and small rivers (e.g., Gordon 1985), T. truncata more typically inhabits medium and large rivers. It also has been reported from lakes and sublotic zones in reservoirs. Little discrimination between substrate types has been observed, but this mussel usually is associated with riffles and flowing water. It has been collected from depths greater than 2 m (Ortmann 1919; Baker 1928; Parmalee 1967; Buchanan 1980).

UNIOMERUS TETRALASMUS

This mussel usually is found in areas with mud or sand bottoms, such as ponds, slow-moving stretches of rivers, lakes, oxbows, sloughs, and ditches. It usually occurs in shallow water (Parmalee 1967). The ability of U. tetralasmus to aestivate during periods of drying enables it to inhabit vernal ponds and streams (van der Schalie 1940).

VILLOSA IRIS COMPLEX

Mussels of this complex inhabit creeks to medium-sized rivers. They generally occur in the vicinity of riffles, although not necessarily in the riffle, and occupy substrate mixtures of sand, gravel, cobble, and occasionally mud or boulder. These mussels sometimes are found in or adjacent to macrophyte beds, occur in areas with bottom currents ranging from slow to swift, and at depths usually less than 1 m (Ortmann 1919; Baker 1928; Parmalee 1967; Buchanan 1980). Clarke and Berg (1959) also record *V. iris* s.s. from sand or gravel bottoms in lakes.

VILLOSA LIENOSA

Although occurring in creeks to medium-sized rivers with sand to cobble substrates, *V. lienosa* may be quite abundant in mud/detritus mixtures, often is associated with macrophyte beds, and occasionally occurs in some large river habitats. Reported depths of occurrence usually are <1 m and current velocities may be calm to moderate, occasionally swift (Clench and Turner 1956).

VILLOSA TAENIATA

This is probably the most commonly encountered *Villosa* species in the Cumberland region. While usually occurring in riffles or flats with sand to boulder substrates, it also may be found in pools or macrophyte beds with mud to sand bottoms. *Villosa taeniata* occurs in areas with calm to swift currents and depths usually <1 m. It inhabits creeks to medium-sized rivers (personal observations).

VILLOSA TRABALIS*

This endangered species has a limited distribution in creeks to medium-sized rivers in the upper Cumberland River basin from the Obey River upstream (Wilson and Clark 1914; U.S. Fish and Wildlife Service 1984d). It usually occurs in the vicinity of riffles with substrates of sand, gravel, and cobble and depths typically less than 1 m. *Villosa trabalis* apparently prefers moderate to swift current velocities but may occupy areas that are seasonally calm. DiStefano (1984) found it in sandy substrate immediately upstream from or along the edge of riffles in slow to moderate flows.

VILLOSA VANUXEMII

This mussel appears to be associated with riffles and flats in creeks to medium-sized rivers. It often will be in the flats above or below riffles and tends to be more common in the smaller streams. Substrates range from sand to heterogeneous mixtures including boulder. *Villosa vanuxemii* occurs at relatively shallow depths and in calm to swiftly flowing water (personal observations).

Table 1. Mussels of the Cumberland River system.

Actinonaias ligamentina (Lamarck 1819)
Actinonaias pectorosa (Conrad 1834)[1]
Alasmidonta atropurpurea (Rafinesque 1820)[1,2]
Alasmidonta marginata Say 1818
Alasmidonta viridis (Rafinesque 1820)
Amblema plicata (Say 1817)
Anodonta grandis Say 1829
Anodonta imbecillis Say 1829
Anodonta suborbiculata Say 1829
Anodontoides ferussacianus (Lea 1834)
Arcidens confragosus (Say 1829)
Cumberlandia monodonta (Say 1829)
Cyclonaias tuberculata (Rafinesque 1820)
Cyprogenia stegaria (Rafinesque 1820)
Dromus dromas (Lea 1834)[1,3]
Ellipsaria lineolata (Rafinesque 1820)
Elliptio crassidens (Lamarck 1819)
Elliptio dilatatus (Rafinesque 1820
Epioblasma arcaeformis (Lea 1831)[1,4]
Epioblasma biemarginata (Lea, 1857)[1,4]
Epioblasma brevidens (Lea 1834)[1,5]
Epioblasma capsaeformis (Lea 1834)[1]
Epioblasma flexuosa (Rafinesque 1820)[4]
Epioblasma florentina (Lea, 1857)[1,3,4]
Epioblasma haysiana (Lea 1833)[1,4]
Epioblasma lenior (Lea 1842)[1,4]
Epioblasma lewisi (Walker 1910)[1,4]
Epioblasma obliquata (Rafinesque 1820)[6,7]
Epioblasma personata (Lea 1829)[4]
Epioblasma stewardsonii (Lea 1852)[1,8]
Epioblasma torulosa (Rafinesque 1820)[6]
Epioblasma triquetra (Rafinesque 1820)
Epioblasma turgidula (Lea 1858)[1,4,6]
Epioblasma walkeri (Wilson and Clark 1914)[1,6]
Fusconaia ebena (Lea 1831)
Fusconaia flava (Rafinesque 1820)
Fusconaia subrotunda (Lea 1831)
Fusconaia undata (Barnes 1823)
Hemistena lata (Rafinesque 1820)
Lampsilis abrupta (Say 1831)[6,9]
Lampsilis cardia Rafinesque 1820[10]
Lampsilis fasciola Rafinesque 1820
Lampsilis ovata (Say 1817)
Lampsilis siliquoidea (Barnes 1823)
Lampsilis teres (Rafinesque 1820)
Lasmigona complanata (Barnes 1823)

(Continued)

Table 1. (Continued)

Lasmigona costata (Rafinesque 1820)
Leptodea fragilis (Rafinesque 1820)
Leptodea leptodon (Rafinesque 1820)
Lexingtonia dolabelloides (Lea 1840)[1]
Ligumia recta (Lamarck 1819)
Medionidus conradicus (Lea 1834)[1]
Megalonaias nervosa (Rafinesque 1820)[11]
Obliquaria reflexa Rafinesque 1820
Obovaria olivaria (Rafinesque 1820)
Obovaria retusa (Lamarck 1819)
Obovaria subrotunda (Rafinesque 1820)
Pegias fabula (Lea 1836)[1,3]
Plethobasus cicatricosus (Say 1829)[3]
Plethobasus cooperianus (Lea 1834)[3]
Plethobasus cyphyus (Rafinesque 1820)
Pleurobema catillum (Conrad 1836)
Pleurobema clavum (Lamarck 1819)
Pleurobema coccineum (Conrad 1836)
Pleurobema cordatum (Rafinesque 1820
Pleurobema gibberum (Lea 1838)[1,2]
Pleurobema oviforme (Conrad 1834)[1]
Pleurobema plenum (Lea 1840)[3]
Pleurobema rubrum (Rafinesque 1820)
Proptera alata (Say 1817)
Proptera capax (Green 1832)[3]
Proptera ohiensis (Rafinesque 1820)
Ptychobranchus fasciolaris (Rafinesque 1820)
Quadrula cylindrica (Say 1817)
Quadrula fragosa (Conrad 1836)
Quadrula metanevra (Rafinesque 1820)
Quadrula nodulata (Rafinesque 1820)
Quadrula pustulosa (Lea 1831)
Quadrula quadrula (Rafinesque 1820)
Quadrula tuberosa (Lea 1840)[1,2]
Simpsonaias ambigua (Say 1825)
Strophitus undulatus (Say 1817)
Toxolasma lividum (Rafinesque 1831)
Toxolasma parvum (Barnes 1823)
Tritogonia verrucosa (Rafinesque 1820)
Truncilla donaciformis (Lea 1828)
Truncilla truncata Rafinesque 1820
Uniomerus tetralasmus (Say 1831)
Villosa iris (Lea 1830) complex
Villosa lienosa (Conrad 1834)
Villosa taeniata (Conrad 1834)[1]

(Continued)

Table 1. (Concluded)

Villosa trabalis (Conrad 1834)[1,3]
Villosa vanuxemii (Lea 1838)[1,8,13]

[1]Cumberlandian regional endemic.
[2]Distribution restricted to the Cumberland River system.
[3]Federally-endangered species.
[4]Presumed extinct (*fide* Stansbery 1981; Bogan and Parmalee 1983).
[5]Recently, *brevidens* Lea 1834, has been considered a junior synonym of *Plagiola interrupta* Rafinesque 1820 (Johnson 1978; Bogan and Parmalee, 1983). These two names do not represent conspecific forms, thus invalidating the subjugation of *Epioblasma* Rafinesque 1831 under *Plagiola* Rafinesque 1820 (unpublished data; Bogan, personal communication).
[6]Recently proposed for federal-endangered status.
[7]*obliquata* Rafinesque 1920 - *sulcata* Lea 1829 (*fide* Johnson 1988; Bogan and Parmalee 1983).
[8]Spelling in accordance with Article 33(d) of the ICZN (Ride, et al. 1985).
[9]This endangered species is listed incorrectly in the Federal Register (1976, vol. 41:24062-24067) as *Lampsilis orbiculata* (Hildreth 1828). Hildreth's species is a synonym of *Obovaria subrotunda* (Rafinesque 1820) see Gordon 1989a).
[10]*cardia* Rafinesque 1820 = *ventricosa* Barnes 1823.
[11]*nervosa* Rafinesque 1820 = *gigantea* Barnes 1823.
[12]*ohiensis* Rafinesque 1820 = *laevissina* Lea 1830 (Gordon, 1989b).
[13]Originally spelled as *vanuxemensis* Lea 1838; recognized as a *lapsus calami* and emendated to *vanuxemii* by Lea (1858). This is in accordance with Article 32(c)ii of the ICZN (Ride, et al. 1985).

Table 2. Mussels that have colonized only the lowland portion of the Cumberland River, downstream from Clarksville, TN.

Anodonta suborbiculata	*Lampsilis siliquoidea*
Arcidens confragosus	*Proptera capax*
Epioblasma flexuosa	*Uniomerus tetralasmus*

Table 3. Mussels reported from upstream of Cumberland Falls.

Actinonaias pectorosa	*Lampsilis cardia*
Alasmidonta atropurpurea	*Lampsilis fasciola*
Alasmidonta marginata	*Lampsilis ovata*
Alasmidonta viridis	*Strophitus undulatus*
Anodontoides ferussacianus	*Toxolasma parvum*
Elliptio dilatatus	

Table 4. Fishes of the Cumberland River system.

Petromyzontidae	
	Ichthyomyzon bdellium (Jordan 1885)
	I. castaneus Girard 1858
	I. greeleyi Hubbs and Trautman 1937
	I. unicuspis Hubbs and Trautman 1937
	Lampetra aepyptera (Abbott 1860)
	L. appendix (DeKay 1842)
	L. meridionale Vladykov, Kott, and Pharand-Coad 1975[1]
Acipenseridae	
	Acipenser fulvescens Rafinesque 1817
Polyodontidae	
	Polyodon spathula (Walbaum 1792)
Lepisosteidae	
	Atractosteus spatula (Lacepede 1803)
	Lepistosteus oculatus Winchell 1864
	L. osseus Linne 1758
	L. platostomus Rafinesque 1820
Amiidae	
	Amia calva Linne 1766
Anguillidae	
	Anguilla rostrata (Lesueur 1817)
Clupeidae	
	Alosa alabamae Jordan and Evermann 1896
	A. chrysochloris (Rafinesque 1820)
	A. pseudoharengus (Wilson 1811)
	Dorosoma cepedianum (Lesueur 1818)
	D. petenense (Gunther 1866)
Hiodontidae	
	Hiodon alosoides (Rafinesque 1819)
	H. tergisus Lesueur 1818
Salmonidae	
	Salmo gairdneri Richardson 1836
	S. trutta Linne 1758[2]
	Salvelinus namaycush (Walbaum 1792)[2]

(Continued)

Table 4. (Continued)

Esocidae	
	Esox americanus vermiculatus (Lesueur 1846)
	E. lucius Linne 1758[2]
	E. masquinongy Mitchill 1824
Cyprinidae	
	Campostoma anomalum (Rafinesque 1820)
	C. oligolepis Hubbs and Green 1935
	Carassius auratus (Linne 1758)
	Clinostomus funduloides Girard 1857
	Ctenopharyngodon idella Valenciennes 1844[2]
	Cyprinus carpio Linne 1758[2]
	Ericymba buccata Cope 1865)
	Hemitrema flammea (Jordan and Gilbert 1878)[1]
	Hybognathus nuchalis Agassiz 1855
	Hybopsis aestivalis (Girard 1857)
	H. amblops (Rafinesque 1820)
	H. dissimilis (Kirkland 1841)
	H. insignis Hubbs and Greene 1956
	H. storeriana (Kirkland 1844)
	Nocomis effusus Lachner and Jenkins 1967
	N. micropogon (Cope 1865)
	Notemigonus crysoleucus (Mitchill 1814)
	Notropis amnis Hubbs and Greene 1951
	N. ardens (Cope 1868)
	N. ariommus (Cope 1868)
	N. atherinoides Rafinesque 1818
	N. blennius (Girard 1857)
	N. boops Gilbert 1884
	N. buchanani Meek 1896
	N. chrysocephalus (Rafinesque 1820)
	N. emiliae (Hay 1881)
	N. fumeus Evermann 1892)
	N. galacturus (Cope 1868)
	N. heterolepis Eigenmann and Eigenmann 1893
	N. leuciodus (Cope 1868)[1]
	N. photogenis (Cope 1865)
	N. rubellus (Agassiz 1850)
	N. shumardi (Girard 1857)
	N. spilopterus (Cope 1868)
	N. stramineus (Cope 1865)
	N. telescopus (Cope 1868)
	N. umbratilis (Girard 1857)
	N. volucellus (Cope 1865)
	N. whipplei (Girard 1857)
	Notropis undescribed from Little South Fork - Palezone shiner[1,3]

(Continued)

Table 4. (Continued)

Notropis undescribed from Little South Fork - Sawfin shiner[1,3]
Phenacobius mirabilis (Girard 1857)
P. uranops Cope 1867[1]
Phoxinus cumberlandensis Starnes and Starnes 1978[1,3]
P. erythrogaster (Rafinesque 1820)
Pimephales notatus (Rafinesque 1820)
P. promelas Rafinesque 1820
P. vigilax (Baird and Girard 1853)
Rhinichthys atratulus (Hermann 1804)
R. cataractae (Valenciennes 1842)
Semotilus atromaculatus (Mitchill 1818)

Catostomidae
Carpiodes carpio (Rafinesque 1820)
C. cyprinus (Lesueur 1817)
C. velifer (Rafinesque 1820)
Catostomus commersoni (Lacepede 1803
Cycleptus elongatus (Lesueur 1817)
Erimyzon oblongus (Mitchill 1814)
Hypentelium nigricans (Lesueur 1817)
Ictiobus bubalus (Rafinesque 1818)
I. cyprinellus (Valenciennes 1844)
I. niger (Rafinesque 1820)
Lagochila lacera Jordan & Brayton 1877
Minytrema melanops (Rafinesque 1820)
Moxostoma anisurum (Rafinesque 1820)
M. carinatum (Cope 1870)
M. duquesnei (Lesueur 1817)
M. erythrurum (Rafinesque 1820)
M. macrolepidotum (Lesueur 1820)

Ictaluridae
Ictalurus furcatus (Lesueur 1840)
I. melas (Rafinesque 1820)
I. natalis (Lesueur 1819)
I. nebulosus (Lesueur 1819)
I. punctatus (Rafinesque 1818)
Noturus elegans Taylor 1969[1]
N. eleutherus Jordan 1877
N. exilis Nelson 1876
N. flavus Rafinesque 1818
N. gyrinus (Mitchill 1817)
N. miurus Jordan 1877
N. nocturnus Jordan and Gilbert 1886
Pylodictis olivaris (Rafinesque 1818)

(Continued)

Table 4. (Continued)

Amblyopsidae	
	Chologaster agassizi Putnam 1872
	Typhlichthys subterraneus Girard 1870
Aphredoderidae	
	Aphredoderus sayanus (Gilliams 1824)
Cyprinodontidae	
	Fundulus catenatus (Storer 1846)
	F. notatus (Rafinesque 1820)
	F. julisia Williams and Etnier 1982
	F. olivaceus (Storer 1845)
Poeciliidae	
	Gambusia affinis (Baird and Girard 1853)
Atherinidae	
	Labidesthes sicculus (Cope 1865)
Percichthyidae	
	Morone chrysops (Rafinesque 1820)
	M. mississippiensis Jordan and Eigenmann 1887)
	M. saxatilis (Walbaum) 1792[2]
Centrarchidae	
	Ambloplites rupestris (Rafinesque 1817)
	Centrarchus macropterus (Lacezede 1802)
	Lepomis auritus (Linne 1758)
	L. cyanellus Rafinesque 1819
	L. gulosus (Cuvier 1829)
	L. humilis (Girard 1858)
	L. macrochirus Rafinesque 1819
	L. megalotis (Rafinesque 1820)
	L. microlophus (Gunther 1859)
	L. punctatus (Valenciennes 1831)
	Micropterus coosae Hubbs and Bailey 1940[2]
	M. dolomieui Lacepede 1802
	M. punctulatus (Rafinesque 1819)
	M. salmoides (Lacepede 1802)
	Pomoxis annularis Rafinesque 1818
	P. nigromaculatus (Lesueur 1829)

(Continued)

Table 4. (Continued)

Percidae	
	Ammocrypta asprella (Jordan 1878)
	A. clara Jordan and Meek 1885
	A. pellucida (Agassiz 1863)
	Etheostoma asprigene (Forbes 1878)
	E. atripinne (Jordan 1877)[1]
	E. baileyi Page and Burr 1982
	E. blennioides Rafinesque 1819
	E. caeruleum Storer 1845
	E. camurum (Cope 1870)
	E. chlorosomum (Hay 1881)
	E. cinereum Storer 1845[1,3]
	E. crossopterum Braasch and Mayden 1985[1,3]
	E. etnieri Bouchard 1977
	E. flabellare Rafinesque 1819
	E. gracile (Girard 1860)
	E. kennicotti (Putnam 1863)
	E. luteovinctum Gilbert and Swain 1887[1]
	E. maculatum Kirkland 1841
	E. microlepidum Rancy and Zorach 1967[1,3]
	E. nigrum Rafinesque 1820
	E. obeyense Kirsch 1892[1,3]
	E. olivaceum Braasch and Page 1979[1,3]
	E. proeliare (Hay 1881)
	E. rufilineatum (Cope 1870)[1,3]
	E. sagitta (Jordan and Swain, 1883)[1,3]
	E. sanguifluum (Cope 1870)[1,3]
	E. smithi Page and Braasch 1976
	E. spectabile (Agassiz 1854)
	E. squamiceps Jordan 1877
	E. stigmaeum (Jordan 1877)
	E. tippecanoe Jordan and Evermann 1890
	E. virgatum (Jordan 1880)[1,3]
	E. zonale (Cope 1868)
	Etheostoma undescribed - Golden snubnose darter[1]
	Etheostoma undescribed - Duskytail darter[1,3]
	Etheostoma undescribed - Stones River darter[1,3]
	Etheostoma undescribed - Jewell darter[1,3]
	Percina burtoni Fowler 1945[1]
	P. caprodes (Rafinesque 1818)
	P. copelandi (Jordan 1877)
	P. evides (Jordan and Copeland 1877)
	P. macrocephala (Cope 1869)
	P. maculata (Girard 1860)
	P. phoxocephala (Nelson 1876)
	P. sciera (Swain 1883)

(Continued)

Table 4. (Concluded)

	P. shumardi (Girard 1860)
	P. squamata (Gilbert and Swain 1887)
	Stizostedium canadense (Smith 1834)
	S. vitreum (Mitchill 1818)
Sciaenidae	
	Aplodinotus grunniens Rafinesque 1819
Cottidae	
	Cottus bairdi Girard 1850
	C. carolinae (Gill 1861)

[1]Cumberland regional endemic.
[2]Introduced.
[3]Restricted only to the Cumberland River basin.

Table 5. Species, periods of spawning,[1] and references to gametogenic cycles for mussels indigenous to the Cumberland River.

Species	Period of ovulation	Reference
Actinonaias ligamentina	July to August	Jirka (1986)
Amblema plicata	mid-June to early July	Stein (1969)
	27 May to 3 August	Holland-Bartels and Kammer (in manuscript)
Anodonta grandis	mid-June to late July	Lewis (1985)
Anodonta imbecillis	several per year	Allen (1924), data in Heard (1975), Hoeh (pers. comm.), Koch (pers. comm.)
Cumberlandia monodonta	late April/early Mayand late October	Gordon and Smith (in press)
Cyclonaias tuberculata	March to June	Jirka (1986)
Elliptio dilatatus	April to June	Jirka (1986)
Lampsilis cardia	16-26 August	Holland-Bartels and Kammer (in manuscript)[2]
Lampsilis fasciola	late August	Zale and Neves (1982a)
Lampsilis siliquoidea	late June to mid-July	Trdan (1981a)
Medionidus conradicus	8-16 July	Zale and Neves (1982a)
Pleurobema cordatum	late April to early May	Yokley (1972b)
Pleurobema oviforme	late March to mid-May	Weaver (1981)
Proptera alata	16 July to 21 August	Holland-Bartels and Kammer (in manuscript)
Quadrula cylindrica	mid-May to mid-June	Yeager and Neves (1986)
Tritogonia verrucosa	March to May	Jirka (1986)

(Continued)

Table 5. (Concluded)

Species	Period of ovulation	Reference
Villosa iris complex	13-20 August	Zale and Neves (1982a)[3]
Villosa vanuxemii	25-30 July	Zale and Neves (1982)

[1]Since the release of sperm may occur before commencement and following cessation of ovulation, spawning is limited to period that ova are discharged through the gonopore.
[2]Presented as *L. ventricosa* in Holland-Bartels and Kammer (in manuscript).
[3]Presented as *V. nebulosa* (Conrad 1834) in Zale and Neves (1982). The *Villosa iris* complex to which *V. nebulosa* appears to group is in need of systematic revision. *Villosa nebulosa* was described from the Alabama River system. The form studied by Zale and Neves (1982) was from the upper Tennessee River drainage and may not be conspecific with *V. nebulosa*.

Table 6. Mussel species known to occur in the Cumberland River basin which may be occasionally hermaphroditic.

Alasmidonta marginata	Pleurobema cordatum
Alasmidonta viridis[2]	Pleurobema rubrum[8]
Anodonta grandis[3,4]	Proptera alata
Cumberlandia monodonta[5]	Proptera ohiensis
Elliptio dilatatus	Ptychobranchus fasciolaris
Fusconaia ebena	Ptychobranchus subtentum
Fusconaia flava[6]	Quadrula quadrula
Lasmigona complanata	Strophitus undulatus
Medionidus conradicus[7]	Titogonia verrucosa
Pleurobema coccineum	Villosa iris

[1]Reference: van der Schalie (1970) unless otherwise indicated.
[2]Ortmann (1911).
[3]As A. hallenbeckii Lea 1858, in Heard (1975) (synonymy fide Hoeh, personal communication).
[4]van der Schalie and Locke (1941).
[5]van der Schalie and Locke (1966).
[6]As Unio rubiginosa Lea 1829, in Sterki (1898).
[7]Zale and Neves (1982).
[8]As U. pyramidatus Lea 1834, in Sterki (1898).
[9]As S. rugosus (Swainson 1822) in van der Schalie (1970).

Table 7. Records of gravidity among mussels known from the Cumberland River (Compiled from Lea 1842, 1863; Sterki 1895; Frierson 1904; Ortmann 1909, 1912, 1913-1916, 1919, 1921, 1923a, 1923b-1924; Conner 1909; Lefevre and Curtis 1912; Surber 1912 1913, 1915; Wilson and Clark 1912a 1914; Howard 1914c, 1915, 1951; Utterback 1915-1916; Baker 1928; van der Schalie 1938; Clarke and Berg 1959; Yokley 1972a; Heard 1975; Clarke 1981, 1985; Trdan 1981; Weaver 1981; Zale and Neves 1982a, 1982b; Bogan and Parmalee 1983; Hill 1986; Jirka 1986; Gordon and Smith, in press; Holland-Bartels and Kammer, in press).

Species	Month											
	J	F	M	A	M	J	J	A	S	O	N	D
Cumberlandia monodonta					X					X		
Fusconaia ebena				X	X	X	X	X	X			
Fusconaia flava			X		X	X	X	X	X			
Fusconaia subrotunda					X	X	X	X				
Fusconaia undata			X	X	X	X	X	X	X			
Megalonaias nervosa	X	X		X	X				X	X	X	X
Amblema plicata					X	X	X	X				
Quadrula cylindrica					X	X	X					
Quadrula fragosa					X							
Quadrula metanevra					X	X	X					
Quadrula nodulata						X	X	X				
Quadrula pustulosa					X	X	X	X				
Quadrula quadrula				X	X	X	X	X				
Quadrula tuberosa[2]												
Tritogonia verrucosa				X	X	X						
Cyclonaias tuberculata				X	X	X	X	X				
Plethobasus cicatricosus[3]												
Plethobasus cooperianus						X	X	X				
Plethobasus cyphyus					X	X	X					
Lexingtonia dolabelloides					X		X					
Pleurobema catillum					X	X	X	X				
Pleurobema clavum					X	X	X	X				
Pleurobema coccineum					X	X	X					
Pleurobema cordatum					X	X	X	X				
Pleurobema gibberum							X	X				
Pleurobema oviforme			X	X	X	X	X					
Pleurobema plenum					X							
Pleurobema rubrum					X	X	X					
Elliptio crassidens				X	X	X	X					
Elliptio dilatatus				X	X	X	X	X	X			
Uniomerus tetralasmus					X			X				
Hemistena lata					X							
Lasmigona complanata	X	X	X	X	X			X	X	X	X	X
Lasmigona costata	X	X	X	X	X			X	X	X	X	X

(Continued)

Table 7. (Continued)

Species	J	F	M	A	M	J	J	A	S	O	N	D
						Month						
Arcidens confragosus	X		X						X			
Anodonta grandis	X	X	X	X	X	X		X	X	X	X	X
Anodonta imbecillis	X	X	X	X	X	X	X	X	X	X	X	X
Anodonta suborbiculata	X	X									X	X
Anodontoides ferussacianus	X	X	X	X	X			X	X	X	X	X
Alasmidonta atropurpurea[10]									X			
Alasmidonta marginata	X	X	X	X	X		X	X	X	X	X	X
Alasmidonta viridis	X	X	X	X	X			X	X	X	X	X
Pegias fabula[10]								X				
Simpsonaias ambigua[11]										X		
Strophitus undulatus	X	X	X	X	X	X	X	X	X	X	X	X
Ptychobranchus fasciolaris	X	X	X	X	X	X		X	X	X	X	X
Ptychobranchus subtentum		X			X				X	X	X	
Obliquara reflexa					X	X	X	X	X			
Cyprogenia stegarla									X	X	X	
Dromus dromas[5]									X	X		
Obovaria olivaria	X	X	X		X	X	X	X	X	X	X	X
Obovaria retusa	X							X	X	X		
Oboaria subrotunda	X	X	X	X	X	X	X	X	X	X	X	X
Actinonaias ligamentina	X	X	X	X	X	X	X	X	X	X	X	X
Actinonaias pectorosa					X				X			
Truncilla donaciformis[7]					X	X	X	X		X		
Truncilla truncata	X	X	X	X	X		X	X	X	X	X	X
Ellipsaria lineolata	X	X	X	X	X	X	X		X	X	X	
Leptodea fragilis	X	X	X	X	X	X	X	X	X	X	X	X
Leptodea leptodon			X						X	X	X	
Proptera alata	X	X	X		X	X	X	X	X	X	X	
Proptera capax						X	X	X		X		X
Proptera ohiensis	X		X		X	X	X	X	X	X	X	
Medionidus conradicus	X	X	X	X	X	X	X	X	X	X	X	X
Toxolasma lividum					X	X	X					
Toxolasma parvum[8]	X				X	X	X	X			X	
Villosa iris	X	X	X	X	X	X	X	X	X	X	X	X
Villosa lienosa		X			X						X	
Villosa taeniata		X		X		X	X		X	X	X	
Villosa trabalis			X								X	
Villosa vanuxemii	X	X	X	X	X	X	X	X	X	X	X	X
Ligumia recta	X	X	X	X	X	X	X	X	X	X	X	X
Lampsilis abrupta	X							X	X	X	X	
Lampsilis cardia	X	X	X	X	X	X	X	X	X	X	X	X
Lampsilis fasciola	X	X	X	X	X	X	X	X	X	X	X	X

(Continued)

Table 7. (Concluded)

Species	Month J	F	M	A	M	J	J	A	S	O	N	D
Lampsilis ovata					X			X	X	X	X	
Lampsilis siliquoidea	X	X	X	X	X	X	X	X	X	X	X	X
Lampsilis teres	X	X	X	X	X	X	X	X		X	X	X
Epioblasma arcaeformis[9]												
Epioblasma biemarginata[9]												
Epioblasma brevidens[9]					X	X						
Epioblasma capsaeformis					X	X	X					
Epioblasma flexuosa[9]									X			
Epioblasma florentina[9]											X	
Epioblasma haysiana[9]											X	
Epioblasma lenior[9]												
Epioblasma lewisi[9]												
Epioblasma obliquata[9]									X	X		
Epioblasma personata[9]									X	X	X	
Epioblasma stewardsonii[9]												
Epioblasma torulosa									X			
Epioblasma triquetra	X	X	X	X	X	X		X	X	X	X	X
Epioblasma turgidula[9]												
Epioblasma walkeri[9]												

[1]Genera are listed in a phylogenetic arrangement following those of Ortmann (1911, 1912, 1925).
[2]Assumed short-term brooder (Heard and Guckert 1970).
[3]Assumed short-term brooder (Bogan and Parmalee 1983).
[4]Assumed short-term brooder (Ortmann 1913-1916).
[5]Assumed long-term brooder (Ortmann 1912, 1921).
[6]Listed as a "winter breeder" by Sterki (1895). The closely related *C. aberti* (Conrad 1850) is a long-term brooder (Chamberlain 1934; unpublished data). Assumed long-term brooder.
[7]Based on extensive year-round observations of numerous individuals, Utterback (1915-1916) suspected that this species may be "tachytictic."
[8]Data on the occurrence of eggs and glochidia in the marsupia (e.g., Ortmann 1919) suggest that populations of *I. parvum* may be short-term or long-term brooders. See text regarding *I. lividum*.
[9]Assumed long-term brooder (Heard and Guckert 1970; Bogan and Parmalee, 1983).
[10]Assumed long-term brooder (Clarke 1981).
[11]Assumed long-term brooder (Baker 1928); however, see Howard (1915).

Table 8. Glochidial morphology of North American Unionoidea.

Taxa	Diagnosis
Margaritiferidae	Small, rounded shells with a row of elongated stylets along inner edge of ventral margin of valves
Amblemidae (non-Proptera)	Small to relatively large, variously shaped (but not triangular) shells, inner edge of ventral margin of valves largely covered with many fine tooth- like projections.
Proptera	Small to medium, rectangular, taller than wide, hinge short, lateral margins concave, ventral margin rounded, inward projecting spines at ventro-lateral junctions
Anodontinae	Relatively large, triangular shells, hinge long, ventral margin pointed with inward projecting hooks composed of microstylets

Table 9. Glochidial hosts for mussels in the Cumberland River basin.

Mussel	Glochidial host	Reference
Actinonaias ligamentina	*Anguilla rostrata*	Coker, et al. (1921)
	Noturus gyrinus	Coker, et al. (1921)
	Morone chrysops	Surber (1913)
	Ambloplites rupestris	Lefevre and Curtis (1910b)
	Lepomis cyanellus	Lefevre and Curtis (1912)
	Lepomis macrochirus	Wilson (1916)
	Micropterus dolomieui	Coker, et al. (1921)
	Micropterus salmoides	Lefevre and Curtis (1910b)
	Pomoxis annularis	Lefevre and Curtis (1912)
	Pomoxis nigromaculatus	Coker, et al. (1921)
	Stizostedion canadense	Coker, et al. (1921)
Alasmidonta marginata	*Catostomus commersoni*	Howard and Ansen (1922)
	Hypentelium nigricans	Howard and Ansen (1922)
	Moxostoma macrolepidotum	Howard and Ansen (1922)
	Ambloplites rupestris	Howard and Ansen (1922)
	Lepomis gulosus	Howard and Ansen (1922)
Alasmidonta viridis	*Etheostoma nigrum*	Clarke and Berg (1959)
	Cottus bairdi	Clarke and Berg (1959); Zale and Neves (1982b)
	Cottus carolinae	Zale and Neves (1982b)
Amblema plicata	*Lepisosteus platostomus*	Coker, et al. (1921)
	Esox lucius	Wilson (1916)
	Carpoides velifer	Howard (1914c)
	Ictalurus punctatus	Howard (1914c)
	Pylodictus olivaris	Howard (1914c)
	Morone chrysops	Wilson (1916)
	Ambloplites rupestris	Stein (1968)
	Lepomis cyanellus	Stein (1968)
	Lepomis gulosus	Howard (1914c)
	Lepomis macrochirus	Howard (1914c)
	Micropterus salmoides	Lefevre and Curtis (1912)
	Pomoxis annularis	Howard (1914c)
	Pomoxis nigromaculatus	Howard (1914c)
	Stizostedion canadense	Surber (1913)
Anodonta grandis	*Atractosteus spatulus*	Wilson (1916)
	Lepisosteus osseus	Trdan and Hoeh (1982)
	Alosa chrysochloris	Surber (1913)
	Dorosoma cepedianum	Wilson (1916)

(Continued)

Table 9. (Continued)

Mussel	Glochidial host	Reference
	Campostoma anomalum	Trdan and Hoeh (1982)
	Cyprinus carpio	Lefevre and Curtis (1910b)
	Notemigonus crysoleucas	Lefevre and curtis (1910b)
	Notropis heterolepis	Trdan and Hoeh (1982)
	Notropis umbratilis	Trdan and Hoeh (1982)
	Pimephales notatus	Trdan and Hoeh (1982)
	Rhinichthys atratulus	Trdan and Hoeh (1982)
	Catostomus commersoni	Kakonge (1972)
	Ictalurus natalis	Wilson (1916)
	Labidesthes sicculus	Trdan and Hoeh (1982)
	Morone chrysops	Wilson (1916)
	Ambloplites rupestris	Lefevre and Curtis(1910b)
	Lepomis cyanellus	Tucker (1928)
	Lepomis macrochirus	Lefevre and Curtis(1910b)
	Lepomis megalotis	Penn (1939)
	Micropterus salmoides	Wilson (1916)
	Pomoxis annularis	Lefevre and Curtis(1910b)
	Pomoxis nigromaculatus	Wilson (1916)
	Etheostoma caeruleum	Trdan and Hoeh (1982)
	Etheostoma nigrum	Hankinson (1908)
	Aplodinotus grunniens	Wilson (1916)
Anodonta imbecillis	*Semotilus atromaculatus*	Clarke and Berg (1959)
	Gambusia affinis	Stern and Felder (1978)
	Ambloplites rupestris	Trdan and Hoeh (1982)
	Lepomis cyanellus	Tucker (1927)
	Lepomis gulosus	Stern and Felder (1978)
	Lepomis macrochirus	Stern and Felder (1978)
	Lepomis megalotis	Parker, et al. (1980)
	Micropterus salmoides	Trdan and Hoeh (1982)
Anodontoides ferussacianus	*Notropis heterolepis*	Kakonge (1972)
	Pimephales notatus	Kakonge(1972)
	Pimephales promelas	Kakonge (1972)
	Catostomus commersoni	Kakonge (1972)
	Cottus bairdi	Clarke and Berg (1959)
Arcidens confragosus	*Anguilla rostrata*	Wilson (1916)
	Dorosoma cepedianum	Surber (1913)
	Ambloplites rupestris	Surber (1913)
	Pomoxis annularis	Surber (1913)

(Continued)

Table 9. (Continued)

Mussel	Glochidial host	Reference
Ellipsaria lineolata	Lepomis cyanellus	Surber (1913)
	Stizostedion canadense	Surber (1913)
	Aplodinotus grunniens	Howard (1914a)
Elliptio crassidens	Alosa chrysochloris	Howard (1914c)
Elliptio dilatatus	Dorosoma cepedianum	Wilson (1916)
	Pylodictis olivaris	Howard (1914c)
	Pomoxis annularis	Howard (1914c)
	Pomoxis nigromaculatus	Howard (1914c)
Epioblasma brevidens	Etheostoma blennioides	Hill (1986)
	Etheostoma maculatum	Hill (1986)
	Etheostoma rufilineatum	Hill (1986)
	Percina caprodes	Hill (1986)
	Cottus carolinae	Hill (1986)
Epioblasma capsaeformis	Etheostoma maculatum	Hill (1986)
	Etheostoma rufilineatum	Hill (1986)
	Percina sciera	Hill (1986)
	Cottus carolinae	Hill (1986)
Epioblasma triquetra	Percina caprodes	Hill (1986)
	Cottus carolinae	Hill (1986)
Fusconaia ebena	Alosa chrysochloris	Surber (1913)
	Lepomis cyanellus	Coker, et al. (1921)
	Micropterus salmoides	Howard (1914c)
	Pomoxis annularis	Howard (1914c)
	Pomoxis nigromaculatus	Howard (1914c)
Fusconaia undata	Lepomis macrochirus	Howard (1914c)
	Pomoxis annularis	Howard (1914c)
	Pomoxis nigromaculatus	Surber (1913)
Lampsilis cardia[3]	Lepomis macrochirus	Coker, et al.(1921)
	Micropterus dolomieni	Coker, et al. (1921)
	Micropterus salmoides	Lefevre and Curtis(1912)
	Pomoxis annularis	Wilson (1916)
	Stizostedion canadense	Wilson (1916)
Lampsilis fasciola	Micropterus dolomieui	Zale and Neves (1982c)

(Continued)

Table 9. (Continued)

Mussel	Glochidial host	Reference
Lampsilis siliquoidea	Noturus gyrinus	Coker, et al. (1921)
	Morone chrysops	Coker, et al. (1921)
	Ambloplites rupestris	Evermann and Clark (1918)
	Lepomis macrochirus	Evermann and Clark (1918)
	Micropterus dolomieui	Coker, et al. (1921)
	Micropterus salmoides	Howard (1914b)
	Pomoxis annularis	Coker, et al. (1921)
	Pomoxis nigromaculatus	Coker, et al. (1921)
	Stizostedion canadense	Coker, et al. (1921)
	Stizostedion vitreum	Coker, et al. (1921)
Lampsilis teres	Lepisosteus osseus	Wilson (1916)
	Lepisosteus platostomus	Howard (1914a)
	Lepomis cyanellus	Surber (1913)
	Lepomis gulosus	Wilson (1916)
	Lepomis humilis	Surber (1913)
	Micropterus salmoides	Wilson (1916)
	Pomoxis annularis	Surber (1913)
	Pomoxis nigromaculatus	Surber (1913)
Lasmigona complanata	Cyprinus carpio	Lefevre and Curtis(1910b)
	Lepomis cyanellus	Lefevre and Curtis(1912)
	Micropterus salmoides	Lefevre and Curtis(1910b)
	Pomoxis annularis	Lefevre and Curtis (1912)
Lasmigona costata	Cyprinus carpio[4]	Lefevre and Curtis(1910b)
Leptodea fragilis	Aplodinotus grunniens	Howard (1912)
Ligumia recta	Anguilla rostrata	Coker, et al. (1921)
	Lepomis macrochirus	Lefevre and Curtis (1912)
	Micropterus salmoides	Lefevre and Curtis (1912)
	Pomoxis annularis	Lefevre and Curtis (1912)
	Stizostedion canadense	Pearse (1924)
Medionidus conradicus	Etheostoma flabellare	Zale and Neves (1982c)
	Etheostoma rufilineatum	Zale and Neves (1982c)
Megalonaias nervosa	Amia calva	Howard (1914c)
	Anguilla rostrata	Surber (1915)
	Alosa chrysochloris	Wilson (1916)
	Dorosoma cepedianum	Howard (1914c)

(Continued)

Table 9. (Continued)

Mussel	Glochidial host	Reference
	Carpoides velifer	Howard (1914c)
	Ictalurus melas	Howard (1914c)
	Ictalurus nebulosa	Coker, et al. (1921)
	Ictalurus punctatus	Howard (1914c)
	Pylodictis olivaris	Howard (1914c)
	Morone chrysops	Howard (1914c)
	Lepomis macrochirus	Howard (1914c)
	Micropterus salmoides	Howard (1914c)
	Pomoxis annularis	Coker, et al. (1921)
	Pomoxis nigromaculatus	Howard (1914c)
	Stizostedion canadense	Howard (1914c)
	Aplodinotus grunniens	Surber (1913)
Plethobasus cyphyus	Stizostedion canadense	Surber (1913)
Pleurobema cordatum	Notropis ardens	Yokley (1972)
	Lepomis macrochirus	Surber (1913)
Pleurobema oviforme	Campostoma anomalum	Weaver (1981)
	Nocomis micropogon	Weaver (1981)
	Notropis cornutus	Kitchel (1985)
	Notropis galacturus	Weaver (1981)
	Notropis leuciodus	Kitchel (1985)
	Notropis telescopus	Kitchel (1985)
	Etheostoma flabellare	Weaver (1981)
Proptera alata	Aplodinotus grunniens	Howard (1912)
Proptera ohiensis	Fundulus notatus[1]	Shira (1913)
	Pomoxis annularis	Surber (1913)
	Aplodinotus grunniens	Coker and Surber (1911)
Quadrula cylindrica	Hybopsis amblops	Yeager and Neves (1986)
	Notropis galacturus	Yeager and Neves (1986)
	Notropis spilopterus	Yeager and Neves (1986)
Quadrula metanevra	Lepomis cyanellus	Surber (1913)
	Lepomis macrochirus	Surber (1913)
	Stizostedion canadense	Howard (1914c)
Quadrula nodulata	Ictalurus punctatus	Wilson (1916)
	Pylodictis olivaris	Coker, et al. (1921)

(Continued)

Table 9. (Continued)

Mussel	Glochidial host	Reference
	Lepomis macrochirus	Howard (1914c)
	Micropterus salmoides	Howard (1914c)
	Pomoxis annularis	Surber (1913)
	Pomoxis nigromaculatus	Howard (1914c)
Quadrula pustulosa	Ictalurus melas	Howard (1912)
	Ictalurus nebulosa	Howard (1914c)
	Ictalurus punctatus	Howard (1912)
	Pylodictis olivaris	Howard (1912)
	Pomoxis annularis	Surber (1913)
Quadrula quadrula	Pylodictis olivaris	Howard and Anson (1922)
Simpsonaias ambigua	Necturus maculosus	Howard (1915)
Strophitus undulatus	Semotilus atromaculatus	Baker (1928)
	Lepomis cyanellus	Ellis and Keim (1918)
	Micropterus salmoides	Baker (1928)
Toxolasma lividum	Lepomis cyanellus	Hill (1986)
	Lepomis megalotis	Hill (1986)
Toxolasma parvum[2]	Lepomis gulosus	Wilson (1916)
Truncilla donaciformis	Stizostedion canadense	Surber (1913)
	Aplodinotus grunniens	Surber (1912)
Truncilla truncata	Stizostedion canadense	Wilson (1916)
	Aplodinotus grunniens	Wilson (1916)
Villosa iris complex	Ambloplites rupestris	Zale and Neves (1982c)
	Micropterus dolomieui	Zale and Neves (1982c)
Villosa vanuxemii	Cottus carolinae	Zale and Neves (1982c)
	Cottus bairdi	Neves, et al. (1985)

(Continued)

Table 9. (Concluded)

[1]Fundulus notatus previously has not been listed as a host of Proptera ohiensis. Shira (1913) found this fish parasitized with glochodia which were similar to but smaller than those of P. capax. Within Shira's (1913) study area, only P. ohiensis posses such glocidia.
[2]Four centrarchid species were listed as glochidial hosts for Toxolasma parvum by Mermilliod (1973; however, these records have not been included because of possible confused identification of T. texasensis as T. parvum.
[3]Fuller (1974) reported glochidial hosts for Lampsilis ovata and L. abrupta (as L. orbiculata). These records actually were for L. cardia and L. higginsii, a species not known from the eastern Interior Basin, respectively.
[4]This exotic species is the only reported host for the widely-distributed Lasmigona costata. Rather than an example of highly restricted host-specificity, this represents a case of unidentified native hosts.

Table 10. Familial affinity of glochidial fish hosts (number of species/family) for mussels of the Cumberland River basin.

Species	Host family															
	Lepisosteidae	Amiidae	Anguillidae	Clupeidae	Escoidae	Cyprinidae	Catostomidae	Ictaluridae	Cyprinodontidae	Poeciliidae	Atherinidae	Perichthyidae	Centrachidae	Percidae	Sciaenidae	Cottidae
Fusconaia ebena				1									4			
Fusconaia undata													3			
Megalonaias nervosa		1	1	2			1	4				1	4	1	1	
Amblema plicata	1				1		1	2				1	7	1		1
Quadrula cylindrica						3										
Quadrula metanevra													2	1		
Quadrula nodulata								2					4			
Quadrula pastulosa								4					1			
Quadrula quadrula								1								
Plethobasus cyphyus														1		
Pleurobema cordatum						1							1			
Pleurobema oviforme						6								1		
Elliptio crassidens				1												
Elliptio dilatatus				1				1					2			
Lasmigona complanata						1							3			
Lasmigona costata						1										
Arcidens confragosus			1				1						2		1	
Anodonta grandis	2			2		8	1	1			1	1	7	2	1	
Anodonta imbecillis						1				1			7			
Anodontoides ferussacianus						3	1									1
Alasmidonta marginata							3						2			
Alasmidonta viridis														1		2
Strophitus undulatus						1							2			
Actinonaias ligamentina			1					1				1	7	1		
Truncilla donaciformis														1	1	
Truncilla truncata														1	1	
Ellipsaria lineolata													1	1	1	
Leptodea fragilis															1	
Proptera alata															1	
Proptera ohiensis									1				1		1	
Medionidus conradicus														2		
Toxolasma lividum													2			
Toxolasma parvum													1			
Villosa iris complex													2			
Villosa vanuxemii																1
Ligumia recta			1										3	1		
Lampsilis cardia													4	1		

(Continued)

Table 10. (Concluded)

Species	Host family															
	Lepisosteidae	Amiidae	Anguillidae	Clupeidae	Escoidae	Cyprinidae	Catostomidae	Ictaluridae	Cyprinodontidae	Poeciliidae	Atherinidae	Perichthyidae	Centrachidae	Percidae	Sciaenidae	Cottidae
Lampsilis fasciola													1			
Lampsilis siliquoidea								1				1	6	2		
Lampsilis teres	2												6			
Epioblasma brevidens														4		1
Epioblasma capsaeformis														3		1
Epioblasma triquetra														1		1

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Appendix A. Representative studies of the aquatic Mollusca of the Tennessee River.

Reference	Subject
Say, 1825	species descriptions (mussels and snails)
Lea, 1824, 1874	species descriptions (mussels and snails)
Conrad, 1834	species descriptions (mussels and snails)
Conrad, 1836-1840	species descriptions (mussels)
Lewis, 1870	species survey (Holston River)
Walker, 1910	species description (Epioblasma lewisi)
Ortmann, 1911	natural history and systematics (mussels)
Boepple and Clark, 1912	species survey (Holston and Clinch rivers)
Ortmann, 1912	anatomy and systematics (mussels)
Ortmann, 1913a-1916	anatomy and systematics (mussels)
Ortmann, 1916	anatomy and systematics (mussels)
Ortmann, 1917	anatomy and systematics (mussels)
Ortmann, 1918	species survey and taxonomy (mussels: Tennessee River)
Ortmann, 1920	morphology and distribution (mussels)
Goodrich, 1921-1941	taxonomy and species descriptions (Pleuroceridae)
Ortmann, 1921	anatomy and systematics (mussels)
Ortmann and Walker, 1922	taxonomy (mussels)
Ortmann, 1924a	species survey and taxonomy (mussels: Duck River)
Ortmann, 1924b	conservation (destruction of fauna at Muscle Shoals)
Ortmann, 1925	species survey and taxonomy (mussels:Tennessee River)

(Continued)

Reference	Subject
van der Schalie, 1939	species survey (mussels: Tennessee River)
Morrison, 1942	species survey (aquatic molluscs: Tennessee River, archeological)
van der Schalie, 1945	conservation (<u>Io</u> <u>fluvialis</u> Say, 1825)
Scruggs, 1960	species survey (mussels: Tennessee River)
Bates, 1962	environmental assessment (mussels: Tennessee River)
Stansbery, 1964	species survey (mussels: Muscle Shoals)
Isom and Yokley, 1968	species survey (mussels: Duck River)
Isom, 1969	species survey (mussels: Tennessee River)
Williams, 1969	species survey (mussels: Tennessee River)
van der Schalie, 1970	hermaphroditism (mussels)
Isom, 1971	species survey (mussels: Tennessee River)
Isom, 1972	species survey (mussels: Tennessee River)
Stansbery, 1972a	species survey (mussels, Pleuroceridae: Holston River)
Stansbery, 1972b	species survey (mussels: Tennessee River, archeological)
Yokley, 1972a	distribution and water quality (mussels)
Isom and Yokley, 1973	species survey (mussels: Flint and Paint Rock rivers)
Isom, et al. 1973	species survey (mussels: Elk River)
Stansbery, 1973	species survey (mussels: Clinch River)
Van der schalie, 1973	species survey (mussels: Duck River)
Stansbery and Clench, 1974	species survey (mussels, Pleuroceridae: Holston River)

(Continued)

Appendix A. (Continued)

Reference	Subject
Stansbery and Clench, 1975	species survey (mussels, Pleuroceridae: Holston River)
Warren, 1975	species survey (mussels: Tennessee River, archeological)
Yokley and Gooch, 1976	environmental assessment (mussels: Tennessee River)
Bates and Dennis, 1978	species survey (mussels: Clinch River)
Johnson, 1978	taxonomic (_Epioblasma_)
Kitchel, et al. 1979	environmental assessment (mussels: Powell River)
Ahlstedt, 1980	conservation (mussels: _Io_: Holston River)
Ahlstedt and Brown, 1980	species survey (mussels: Powell River)
Ahlstedt, 1981	species survey (aquatic molluscs: Duck River)
Clarke, 1981	taxonomic (Alasmidontini)
Dennis, 1981	species survey (mussels: Powell River)
Pardue, 1981	species survey (mussels: Tennessee River)
Weaver, 1981	natural history (_Pleurobema_ _oriforme_: Big Moccasin Creek)
Ahlstedt, 1982	species survey (aquatic molluscs: Copper Creek)
Jenkinson, 1982	endangered species (mussels: Tennessee River system)
Zale and Neves, 1982a	reproductive biology (mussels)
Zale and Neves, 1982b,c	glochidial host determination
Ahlstedt, 1983	species survey (aquatic molluscs: Elk River)
Clarke, 1983	species status survey (mussels, Pleuroceridae)

(Continued)

Appendix A. (Continued)

Reference	Subject
Ahlstedt, 1984	species survey and natural history (mussels: Clinch River)
Dennis, 1984	species survey and environmental assessment (mussels: Tennessee River)
Parmalee and Klippel, 1984	species survey (mussels: Tellico River)
Clarke, 1985	taxonomic (Alasmidontini)
Kitchel, 1985	natural history (Fusconaia cor: North Fork Holston River)
Neves, et al. 1985	glochidial host determination
Ahlsted, 1986a	species status survey (Pegias)
Ahlsted, 1986b	species survey (mussels: Tennessee River system)
Barr, et al. 1986	habitat characterization (mussels: Tennessee River system)
Casey, 1986	species survey (mussels: Tennessee River, archeological)
Hill, 1986	glochidial host determination
Koch, et al. 1986	glochidial host determination
Sheehan, et al. 1986	conservation (mussels: Clinch and North Fork Holston rivers)
Yeager and Neves, 1986	glochidial host determination
Neves and Widlak, 1987	ecology (mussels)
Bruenderman, 1988	natural history (Fusconaia cuneola: Clinch River)
Jenkinson, 1988	species survey (mussels: Duck River)
Jenkinson and Ahlstedt,1988a	species survey (mussels: Clinch River)
Jenkinson and Ahlstedt, 1988b	species survey (mussels: Powell River)

(Continued)

Appendix A. (Concluded)

Reference	Subject
Neves and Widlak, 1988	reproductive biology (mussels)
Dennis, 1989	species survey (mussels: Clinch River)

Appendix B. Representative surveys of freshwater mussels from the Cumberland River system.

Reference	Subject
Williamson, 1905	Rockcastle River
Wilson and Clark, 1914	Cumberland River below Cumberland Falls, various tributaries
Shoup and Peyton, 1940	Big South Fork Cumberland River
Shoup, et al. 1941	Obey, Wolf, and adjacent stretches of Cumberland rivers
Neel and Allen, 1964	Kentucky portion of the upper Cumberland River basin
Stansbery, 1969	Cumberland Falls
Blankenship and Crockett, 1972	Rockcastle River
Tennessee Valley Authority, 1976	upper Old Hickory Reservoir (Cumberland River)
Parmalee, et al. 1980	upper Old Hickory Reservoir (Cumberland River, recent and archeological)
Call and Parmalee, 1982	records for Alasmidonta atropurpurea (upper Cumberland River basin)
Sickle, 1982	lower Cumberland River below Barkley Dam
Starnes and Bogan, 1982	Little South Fork Cumberland River
Clarke, 1983	scattered localities in Cumberland River basin
Hickman and Ahlstedt, 1983	upper Old Hickory Reservoir, (Cumberland River)
DiStefano, 1984	Horselick Creek
Miller, 1984	lower Caney Fork Cumberland River
Miller, et al. 1984	Cumberland River between Cumberland Reservoir and TN/KY border
Thompson, 1985	Rockcastle River

(Continued)

Appendix B. (Concluded)

Reference	Subject
Ahlstedt, 1986a	status survey of _Pegias fabula_
Casey, 1986	lower Cumberland River basin
Sickle, 1987	mouth of the Cumberland River
Schuster, 1988	Cumberland River basin in Kentucky
Starnes and Bogan, 1988	Cumberland River basin in Tennessee
Schmidt, et al. 1989	Stones River
Anderson, et al. in press	Little South Fork Cumberland River
Schuster, et al. in press	Buck Creek

Appendix C. Early mussel resources surveys conducted by the U.S. Bureau of Fisheries.

Reference	Subject
Clark and Gillette, 1911	Little Arkansas River, Kansas
Boepple and Coker, 1912	Holston and Clinch rivers, Tennessee
Meek and Clark, 1912	Buffalo River, Arkansas
Wilson and Clark, 1912a	Kankakee River, Indiana and Illinois
Wilson and Clark, 1912b	Cumberland River, Kentucky and Tennessee
Wilson and Clark, 1912c	upper Wabash and Maumee rivers
Wilson and Danglade, 1912	rivers in Minnesota
Shira, 1913	Cypress and Sulphur rivers, Texas and Louisiana
Danglade, 1914	Illinois River, Illinois
Eldridge, 1914	Fox River, Illinois
Isely, 1914a	various rivers, eastern Oklahoma
Utterback, 1914	rivers in Missouri
Wilson and Clark, 1914	Cumberland River, Tennessee and Kentucky
Wilson and Danglade, 1914	rivers in Minnesota
Coker, 1915	Tenas River, Louisiana
Coker and Southall, 1915	upper Missouri River tributaries
Danglade, 1922	Kentucky River, Kentucky
Grier, 1922	upper Mississippi River
Grier and Mueller, 1922	upper Mississippi River
Isely, 1925	various rivers, eastern Oklahoma
Southall, 1925	Lake Pepin, upper Mississippi River
Grier, 1926a	upper Mississippi River
Coker, 1929	Mississippi River, Keokik, Iowa

Appendix D. Early studies on mussel production, propagation, and glochidial host identification conducted by the U.S. Bureau of Fisheries.

Reference	Subject
Lefevre and Curtis, 1910a	reproductive biology and propagation
Lefevre and Curtis, 1910b	reproductive biology
Coker and Surber, 1911	gluchidial metamorphosis
Lefevre and Curtis, 1911	non-parasitic glochidial metamorphosis
Young, 1911	glochidial parasitism in fish
Howard, 1912	glochidial host identification
Lefevre and Curtis,1912	reproductive biology and propagation
Surber, 1912	gravidity records and glochidial identification
Surber, 1913	glochidial host identification
Howard, 1914a	glochidial host identification
Howard, 1914b	propagation
Howard, 1914c	reproductive biological host identification
Howard, 1914d	non-parasitic glochidial metamorphosis
Isely, 1914b	shell production
Churchill, 1915	nutrient consumption
Howard, 1915	reproductive biology and host identification
Surber, 1915	glochidial identification
Churchill, 1916	nutrient consumption
Wilson, 1916	fish immunity to glochidial parasitism
Howard, 1917	propagation
Coker, et al. 1921	natural history

(Continued)

Appendix D. (Concluded)

Reference	Subject
Howard, 1922	propagation
Howard and Anson, 1922	reproductive biology
Blystad, 1923	glochidial parasitism
Churchill and Lewis, 1924	nutrient consumption
Ellis and Ellis, 1926	propagation
Ellis and Ellis, 1927	nutrient consumption
Ellis, 1929	shell production
Isely, 1931	shell production
Chamberlain, 1934	reproductive biology and glochidial parasitism
Howard, 1951	glochidial host identification
Howard, 1953	non-parasitic glochidial metamorphosis

Appendix E. Representative recent studies in life history, ecology, and conservation of freshwater mussels.

Reference	Subject
Clarke, 1970	endangered species
Jorgensen and Sharp, 1971	endangered species
Yokley, 1972	life history and glochidial host
Heard, 1975	reproductive biology
Coon, et al. 1977	production
Fuller, 1978	ecology and natural history
Kitchel, et al. 1979	environmental assessment and endangered species
Green, 1980	production
Vannote, et al. 1980	ecological modelling
Strayer, 1981	ecological
Strayer, et al. 1981	production
Weaver, 1981	reproductive biology and glochidial host identification
Bronmark and Malmqvist, 1982	ecological
Isom and Hudson, 1982	propagation
Miller, 1982	natural history, conservation, and endangered species
Vannote and Minshall, 1982	ecological modelling
Zale and Neves, 1982a,b,c	reproductive biology and glochidial host identification
Miller, 1983	natural history, conservation, and endangered species
Strayer, 1983	ecological
Isom and Hudson, 1984	reproductive biology
Kitchel, 1984	ecological

(Continued)

Appendix E. (Concluded)

Reference	Subject
Moyer, 1984	production
Sylvester, et al. 1984	natural history and endangered species
Kitchel, 1985	natural history and endangered species
Neves, et al. 1985	glochidial host identification
Wiles, 1985	glochidial host identification
Cumberlandian Mollusk Conservation Program	
Ahlstedt, 1986b	biogeography
Barr, et al. 1986	faunal association
Hill, 1986	glochidial host identification
Isom, 1986	propagation
Jenkinson and Heuer, 1986	environmental assessment
Koch, et al. 1986	glochidial host identification
Ostrowski and Speaks, 1986	environmental assessment
Poppe and Fehring, 1986	environmental assessment
Wade and Webb, 1986	environmental assessment
Jirka, 1986	reproductive biology and production
Sheehan, et al. 1986	conservation
Yeager and Neves, 1986	reproductive biology and glochidial host identification
Neves, 1987	conservation
Neves and Widlak, 1987	natural history
Bruenderman, 1988	reproductive biology and endangered species
Holland-Bartels and Waller, 1988	natural history and endangered species

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15. Supplementary Notes

16. Abstract (Limit: 200 words)

This report provides a synopsis of the information available on the life histories of the mussels of the Cumberland River basin. There are detailed sections on reproductive strategies and habitat utilization. A separate section describes the habitat preferences of individual species. This synopsis of the literature will be useful to biologists with various interests, including taxonomists, ecologists, and those involved in assessing mussel habitats and the impacts of water development projects and land-use practices on these habitats.

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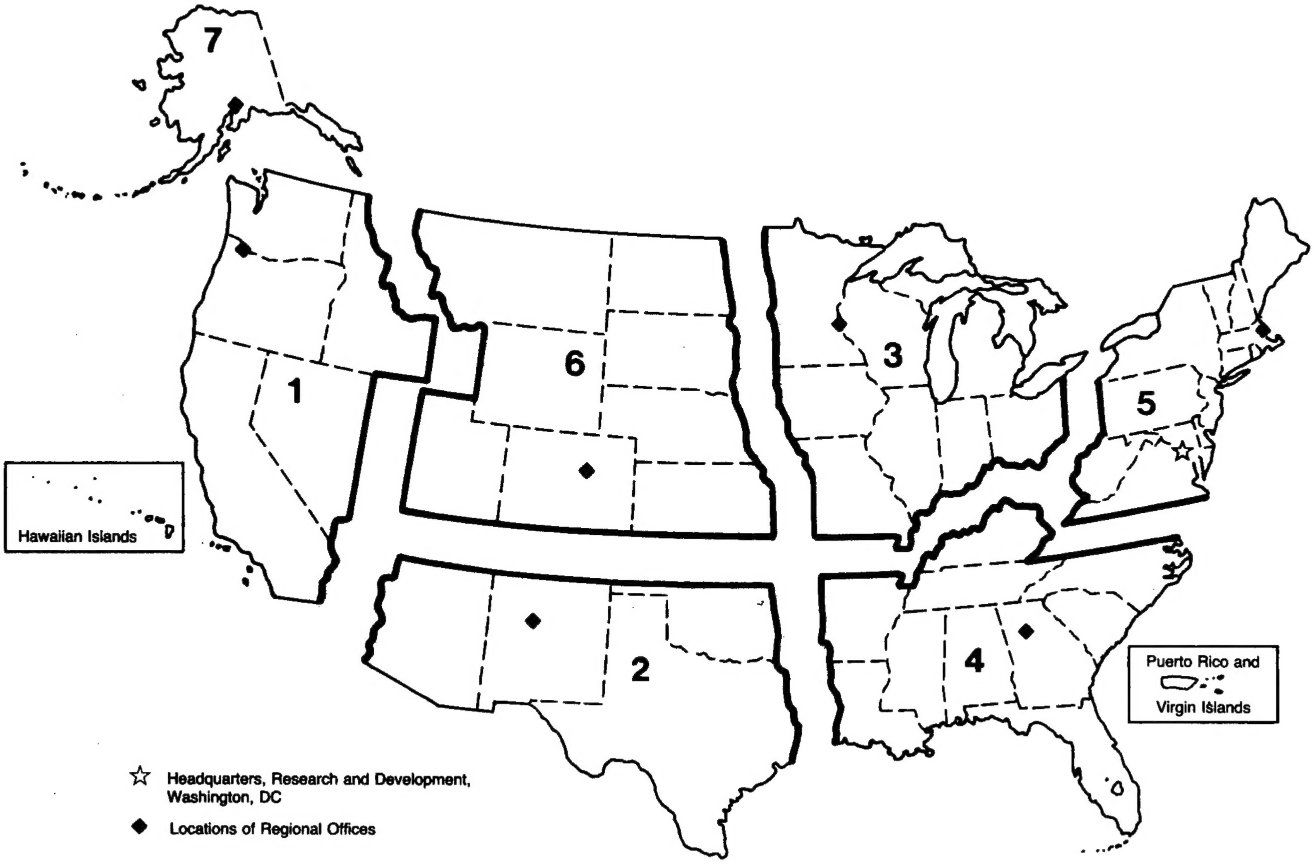

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INT-423